Circadian Rhythms and Melatonin Receptors as Sources of Individual Variation in Reproductive Photoresponsiveness

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ORPHIC DESCENT IN LORD JIM

A Thesis

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In Partial Fulfillment

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Master of Arts

by

Sonya Willie

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Master of Arts

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Approved, May 2001

Chris Bongie

Richard Lowry

Thomas Heacox
In loving memory of James Henry Willie.
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ABSTRACT

In this thesis, I am attempting to investigate how Joseph Conrad's artistic manifesto as expressed in the Preface to The Nigger of the 'Narcissus' (1897) works itself out in his novel Lord Jim (1900); more specifically, I am examining the way in which the Preface's equating of artistic process with descent—a descent that I argue is Orphic in nature—is illustrated in the pattern of descents that constitutes Lord Jim. In Lord Jim, Orpheus becomes a metaphor for both art and existence, for modern consciousness and the paradoxically simultaneous relativity and universality of truth.

I began this study hoping that a close mythic reading of Lord Jim would resolve the paradoxes of the text and affirm the structural integrity of the novel that I presumed was to be found behind the veil of its apparent dis-integration of conventional nineteenth-century narrative forms. I was surprised to find that approaching the concept of Orphic descent in the substructure of the text was merely a starting point for a larger and less resoluble project. Orphic descent is, indeed, technically and thematically integral to the structure of the novel, its impressionistic narrative technique, and the heroic code it attempts (but fails) to assert; however, a close mythic reading of the text, far from resolving many or even any of the paradoxes in the text, only compounds them, leaving the text's mysterious multiplicity intact. Orphic descent in the novel provides not the unifying myth I first suspected it would, but rather a way for Conrad of understanding the lack of such a myth and of the unity, and lifting of the veil, that such a myth might be thought to provide.

Orphic descent figures into Conrad's consistently voiced rhetoric of enigma: the Orphic artist speaks about Truth but does not reveal it; gestures toward a Unity, but always in a language that resists unification. Myth becomes not a solution to the problem of disunity, but a way of exploring that problem. It is the exploration of this problem, rather than any solution to it, that has engaged me in this thesis.
ORPHIC DESCENT IN LORD JIM
Since it is not given to man to solve the mystery of existence, he must learn his limitations by looking into the mirror of mankind, which will unite him in compassion, pity, and love for all men, who are perishing in the supreme disaster.

(Robert Andreach, 39)

(i) Introduction: The Modern Relevance of Conrad’s Artistic Descents and Mythic Substructure

Joseph Conrad, Polish expatriate and former sailor, embarked upon a career as a writer at the close of the nineteenth century—a time when sailing ships were being replaced by steam and when the progress of imperialism was destroying the exotic. The century saw highly concentrated advancements in psychology, science, and technology. The sheer mass of new ideas undermined the old, suspending traditional belief systems and values. The literature of the period—mirroring the modern experience—adopts this suspension of traditional forms and values; “there is the strong sense that relativism and increasing subjectivism had made all things false, revealed the old standards and forms as so many hollow idols” (White, 64). Early modern novelists experimented with language and form, seeking new methods to communicate and order the chaos of their changing and bewildering time. Myth and ritual, according to Clyde Kluckholn, “supply... fixed points in a world of bewildering change and disappointment” (Kluckholn, 68), for primitive and modern man alike. Undertones of myth and ritual provide the modern writer with a method of structuring the chaos of modernity by suggesting universal themes in an increasingly relativized world. This use of myth and ritual—so fundamental to the vision of high
modernists like Joyce and Eliot—is vitally present in the work of the early modernist novelist, Joseph Conrad.

In this thesis, I am attempting to investigate how Joseph Conrad’s artistic manifesto as expressed in the Preface to The Nigger of the ‘Narcissus’ (1897) works itself out in his novel Lord Jim (1900); more specifically, I am interested in examining the way in which the Preface’s equating of artistic process with descent—a descent that I argue is Orphic in nature—is illustrated in the pattern of Orphic descents that constitutes Lord Jim. Not long before Joyce chooses Daedalus as his archetypal artist, Conrad chooses Orpheus as his. In Lord Jim, Orpheus becomes a metaphor for both art and existence, for modern consciousness and the paradoxically simultaneous relativity and universality of truth. Orphic descent provides the rhetorical device through which Conrad approaches but never reveals ultimate truth—the enigma behind the veil of the visible world.

I began this study hoping that a close mythic reading of Lord Jim would resolve the paradoxes of the text and affirm the structural integrity of the novel that I presumed was to be found behind the veil of its apparent dis-integration of conventional nineteenth-century narrative forms; I also hoped (and I still do hope) to confirm, contradict, and complement other critical interpretations through my exploration of Orphic descent as integral to the mythic substructure of the novel. However, just as Conrad was surprised to find that his original idea for a short story centered around what would eventually become the Pilgrim ship episode of Lord Jim had turned into “a good starting-point for a free and wandering tale...an event, too, which could conceivably colour the whole ‘sentiment of existence’ in a simple and sensitive character” (Conrad, Lord Jim [henceforth referred to only by page number] 1), I was surprised to find that approaching the concept of Orphic descent in the substructure of the text was merely a starting point for a larger and less resoluble project. As I had first suspected, Orphic descent is, indeed, technically and thematically integral to the structure of the novel, its impressionistic narrative technique, and the heroic code it attempts (but fails) to assert; however, as it turned out, a close mythic reading of
the text, far from resolving many or even any of the paradoxes in the text, only ended up compounding them, leaving the text's mysterious multiplicity intact. Indeed, Orphic descent in the novel provides not the unifying myth I first suspected it would, but rather a way for Conrad of understanding the lack of such a myth and of the unity, and lifting of the veil, that such a myth might be thought to provide. Orphic descent figures into Conrad's consistently voiced rhetoric of enigma: the Orphic artist speaks about the Unspeakable but does not reveal it; gestures toward a Unity, but always in a language that resists unification. Myth becomes not a solution to the problem of disunity, but a way of exploring that problem—and it is in this respect that Conrad's use of myth is typically modernist. Modernists recognize, as Frederick Karl has argued, that "in the interstices of knowledge there lies an entire universe of unchartables...in the seams of all these abundant data, there are other data that have no coordinates except in the mind of the artist" (Karl, 72). Conrad's "disaffected," Orphic artist "is the only one who can, verbally, visually, aurally, bring together these multiplicities that make modern life so compartmentalized" (Karl, 72)—and yet, as I found, this bringing together of a "universe of unchartables" is only possible through an acknowledgment of the relative, non-universal nature of modern life.

The mythic substructure of Conrad's *Lord Jim* reenacts the death of Western tradition and modern man's subsequent quest for renewal. Robert Andreach best explains Conrad's modern predicament:

> the old God is dead and since science and materialism fail to give a satisfying new One, Western man, cut off from his past, is an abandoned derelict in a universe which, constantly stirring his surviving primitive religious instinct, invites him to uncover the mystery behind the veil of the visible world. (210)

In response to this dilemma, Conrad creates an innovative hero and artist, Charlie Marlow, through whom Conrad seeks "to uncover the mystery behind the veil of the visible world" via Orphic descent and return. Conrad—like Nietzsche's myth-less man—is "eternally hungering among all the bygones" of Romantic individualism for the passion and meaning that mark
Romantic wonder (Nietzsche, 109). In his short stories and novels, Conrad constantly “digs and grubs for roots, though he have to dig for them even among the remotest antiquities” (Nietzsche, 109). In Lord Jim, Conrad’s descending narrator, Marlow, digs for “fixed points,” or “roots,” to overcome the sense of isolation and loss of value associated with modernity.

Marlow is the secondary narrator in the short story, “Youth” (1898), the novella, Heart of Darkness (1899), and the novel Lord Jim (1900). All three Marlovian tales—which Conrad originally intended to publish together—explore the heroic and artistic quest in an atmosphere loaded with myth and ritual. Marlow descends in each work, emerging each time with a progressively longer and more complicated tale as Conrad progresses from the story to the novella to the novel. In “Youth,” Marlow descends to a younger Marlow, a Romantic dreamer much like Jim, and describes his naïve response to the sinking of his first ship. A little bit older in Heart of Darkness, Marlow as narrator not only descends to an earlier version of his self as character, but also to the destructive egoist Kurtz, and emerges transformed. Lord Jim’s middle-aged Marlow encounters a younger version of himself and of Kurtz in Jim, as well as in a series of descending and confessing character doubles. Each Marlovian adventure incorporates the mythic substructure of the heroic quest for maturity through rituals of descent, confession, and writing. Lord Jim—the largest and final installment of his early Marlovian trilogy (Marlow will, of course, reappear in the much later Chance [1913])—puts into play the densest mythic substructure and the most complexly interwoven descending and confessing heroes and artists in an impressionistic redefinition of modern values.

In the mythic substructure of Lord Jim, Conrad re-creates and recombines the descent of the mythic hero and Christian and Orphic mythology in a complex juxtaposition of heroism and artistry. Lord Jim is an amalgamation of mythic elements and evocative settings, in which multiple heroes and artists reenact creation, the fall, and the redemption of mankind. Jim falls—descends from the Patna—then descends into Patusan and creates an alternative identity as a Lord, redeeming himself in his own eyes; Marlow, recreating Jim and reenacting Jim’s descents
through his tale, is left the task of determining the true redemptive value of Jim’s self-destruction. Both Christ-like Jim, who sacrifices himself to atone for his errors, and Orphic Marlow, who descends and returns with a tale, are artists for whom descent is integral to creation and renewal.

Orphic and Christian allusions are the predominant mythic elements in *Lord Jim*: Conrad uses these mythic heroes to indicate the inadequacy of Christian tradition for modern man and to sacralize the role of the artist (as embodied by Orpheus) in an impressionistic effort at modern mythmaking and renewal. Conrad replaces the Christian paradigm with the Orphic, rendering sacred the artist as the hero who fulfills man’s needs for wonder and for solidarity through patterns of descent and return. For Conrad, the artist *is* the hero, descent is necessary for creation and regeneration, and striving for solidarity is the only answer to modern isolation. Walter Strauss clarifies the importance of the transformation of the Orphic poet as a result of his descent:

> the Orphic poet seeks to regenerate himself particularly by means of the voyage downward, with its attendant self-recognition through remembrance and its mandatory self-transformation, followed by return to the world that will become the ground of a vaster metamorphosis. (Strauss, 13)

In each text of the Marlovian trilogy, Conrad’s paradigmatic artist, Marlow, is transformed by his descent. In *Lord Jim*, while Jim himself never acquires self-knowledge, Marlow recognizes himself in Jim, and leaves Patusan with an altered consciousness. As a result of Jim’s experiences on the *Patna* and in Patusan, Marlow changes his (and by extension the reader’s) ideas of heroism and of how to be. Jim’s fall from moral security parallels that of Marlow, that of Conrad, and that of Conrad’s modern audience. Jim’s Romantic form of renewing his link with society is paradoxical self-destruction; Marlow’s modern form of renewing his link with society (and with his reader) is his Orphic tale telling. Conrad repeatedly explores this dialogue between romance and modernity, leading the reader of *Lord Jim* through the mythic and psychological milieu of its disrupted narratives to an impression of solidarity.
In telling Jim's tale, Marlow recounts his own spiritual journey, along with the accounts of other narrators who provide diverse perspectives on the same tale. Marlow's narrative is broken and filled in intermittently—and never in chronological order—by disparate narrators, including the Patna engineer, Chester, Brierly, Brierly's first mate, the French Lieutenant, Brown, Jewel, and Tamb Itam, to name a few. This complex diffusion of doubled characters and narrators and the interwoven patterns of plural descents that results from it inextricably links, as we will see, Conrad's aesthetics of artistry with his code of heroism. Each teller, frequently a hero or artist who doubles either Marlow or Jim or both, not only reveals a truth about Jim but also reveals truths about human nature, human experience, and the place (or lack thereof) of heroism in the world of Lord Jim. This fragmentation of truth suggests the relativism of modern experience and any or all moral codes.

Conrad's fragments of truth and succession of tellers also reiterate the importance of tale-telling in structuring truth or reality. Each blatant shift in tellers conveys the vital role of the subjective teller, or artist, in heroically ordering the chaos of modernity and determining what is sacred:

The Orphic poet is, once more, at the beginning of a journey, confronted with the task of sacralizing time, space, and language before the Orphic spell can take place. His task is to face the Nothingness, to overcome (abolish) it in order to make poetry once more possible. (Strauss, 12)

Marlow's journey is a continuous effort to confront this Nothingness; he doggedly retraces the path of Jim's absence until it ends with Jim's death. Frederick Karl explains the desacralization of the modern world—the disruption of the "continuum" of man, nature, and history—as the result of the splitting off of words into new roles, "the separation of things and the languages to express them" (69). Of all the doubled heroes and descending artists in Lord Jim, only Marlow's Orphic descent and return overcomes the Nothingness in order to make "poetry" (as embodied by Jim) once more possible. The interminable disruptions of the tale by various tellers define Jim as the
sum total of his absences: he becomes a receding truth produced by the “collective memory” (Karl, 309) of the multiple descents and various tellers.

The layered artistic descents (or states of consciousness) of Lord Jim are analogous to the experience of the artist as described within Joseph Conrad’s Preface to The Nigger of the ‘Narcissus’. This Preface identifies the object of literary craftsmanship and artistic descent as an appeal to the reader’s subconscious that will establish solidarity with the reader:

The artist, then, like the thinker or the scientist, seeks the truth and makes his appeal....

Confronted by the same enigmatical spectacle the artist descends within himself, and in that lonely region of stress and strife, if he be deserving and fortunate, he finds the means of his appeal. His appeal is made to our less obvious capacities: to that part of our nature which, because of the warlike conditions of existence, is necessarily kept out of sight within the more resisting and hard qualities.... But the artist appeals to that part of our being which is not dependent on wisdom... to the subtle and invincible solidarity...which binds together all humanity—the dead to the living and the living to the unborn. (Conrad, Prefaces, 49-50)

Conrad’s comments relating creation and renewal to the human subconscious here are extremely relevant to the patterns of descent in Lord Jim. Conrad appropriates the subconscious as the realm of the artist. Exiled subsequent to the Patna incident, Jim enters the “lonely region of stress and strife” associated with the heroic quest. Despite Jim’s exile and flight, Marlow continually affirms that Jim is “one of us” (57), part of the society of men which includes the reader. Marlow’s devotion to Jim and compulsion to tell his tale evokes the importance of tale telling in promoting human solidarity. Jim, hardly a paragon of “wisdom,” and certainly associated with the subconscious depths, is the means of Marlow’s appeal to his audience and of Conrad’s appeal to his reader. Not only does Marlow identify with Jim, so does the reader. In Jim, the reader recognizes the naïve egoism of his own youth.
Several passages in particular describe this subconscious appeal of Jim and invoke his enigmatic nature: early on in the novel, for instance, we are told that he appeals "to all sides at once—to the side turned perpetually to the light of day, and to that side of us which, like the other hemisphere of the moon, exists stealthily in perpetual darkness, with only a fearful ashy light falling at times on the edge" (57). Jim is the invaluable gem hidden in the universal subconscious; he embodies the subconscious need for Romantic wonder, and as such he connects "the dead to the living and the living to the unborn." In a later passage, the parable spoken by master artist Stein implies the importance of universal man’s subconscious needs to his conscious survival and links artistic descent to a metaphor for existence. Stein’s parable diagnoses the Romantic’s need to immerse himself in the destructive element in order to survive. Crucial in any discussion of the symbolic layering of artistic descent in Lord Jim, Stein’s diagnosis subtly parallels both the modern existential dilemma and Jim’s personal dilemma, as well as Conrad’s evocation of artistic descent in the Preface to The Nigger of the ‘Narcissus’. Invoked in Stein’s parable are enigmatic metaphors involving the sea and the dream into which man is born or falls. Stein reiterates the importance of descent and submission in surviving the destructive elements of existence/artistry:

...A man that is born falls into a dream like a man who falls into the sea. If he tries to climb out into the air as inexperienced people endeavour to do, he drowns—nicht wahr...No! I tell you! The way is to the destructive element submit yourself, and with the exertions of your hands and feet in the water make the deep, deep sea keep you up. So you ask me—how to be? (130)

For Stein, and for Conrad, existence has become the task, or art, of creating one’s own system of meaning in the face of modernity. Stein indicates that the inexperienced person will self-destruct by resisting his nature and by struggling against his natural element, an element Stein associates with water and with dreams. The way to survive, by contrast, is to submit to this watery, subconscious element in which one is immersed so that one is sustained rather than destroyed by it. This watery baptism, symbolic of death and rebirth, suggests the rebirths necessary for man to
actualize his potential: burying Jim in Patusan is, for Stein, “something practical” (131), and necessary for his rebirth.

Because Stein’s truth is directly applied to the situation of Jim, that of an exile in need of personal exoneration, his parable conveys to the modern reader the need for personal redemption and solidarity. Jim’s “world pain” (130) is caused by his break from society, a break that he chooses to repeat at the end of the novel (as Robert Andreach has emphasized) when he sacrifices himself in Patusan. Capitulating to Doramin’s avenging bullet, Jim is fully immersed in the destructive element of his dreams. Not until this ultimate immersion in the destructive (but also, at least for Marlow and the reader, redemptive) element does Jim finally seem joined with the Eurydice-like Eastern bride whose ghostly presence, as we will now see, accompanies him on his quest to realize his Romantic dreams throughout the novel. In Patusan, Christ-like Jim becomes a hero and an artist, a slain god speaking to our conscious and subconscious needs for wonder, resurrected by his most obvious doubles, God-like Stein and Orphic Marlow.
(ii) Orphic Descent and Eastern Brides

David Lynn has argued—and I agree—that anyone seeking a resolution to the paradoxes that lie at the heart of *Lord Jim*, is following a misguided impulse (Lynn, 45); Conrad’s novel defies a closed interpretation because the meaning undergoes an Orphic metamorphosis for each reader and each critic at each reading. With each reader the quest goes on, because “strictly speaking, a ‘quest’ is never geared to success; its (etymological) essence lies in ‘seeking’—not in attaining at some point in the future that which is being sought” (Bongie, 21). As my recourse to the idea of “Orphic metamorphosis” demonstrates, I will be seeking to understand (if not resolve) the novel’s paradoxes by emphasizing its mythic and ritualistic dimensions. Through the course of this study, I will have occasion to refer to a number of Conrad critics who have taken this approach to his work: notably, Joseph Dobrinksy, David Lynn, Robert Andreach, Walter Strauss, and Deborah Guth. No critic, though, has contributed more to this line of interpretation than Albert J. Guerard in his seminal study *Conrad: The Novelist*, where he noted Conrad’s fixation with spiritual and moral isolation and first recognized in Conrad’s sea voyages and Congo journey the anthropological and psychological concept of “the night journey” (Guerard, 15) into the realm of the subconscious.

The night journey—what I refer to as descent—is apparent in all three Marlovian explorations of spiritual or moral isolation. For Guerard, Conrad’s night journey is an archetypal myth of spiritual redefinition, the “story of an essentially solitary journey involving profound spiritual change in the voyager… [whose] journey is a descent into the earth, followed by a return to light” (Guerard, 15). Careful to avoid Jung’s system of symbols for the unconscious even as he applies Jungian psychoanalytic methodology, Guerard likens this myth to a universal dream caused by “certain psychic needs” which result from conscious and unconscious living—the psychic needs
of modern living. Conrad was exceptionally attuned to the cost of modern living: he knew, in the words of Haskell M. Block, that "Civilization has its price, not the least of which is the extinction of mystery and the impoverishment of wonder" (Block, 52). Conrad returns to myth and ritual—to Orphic descent and return—to explore the Romantic roots of wonder, to define a new mythology, and to create a new but definitely familiar type of hero.

Orphic myth throughout the ages links Orpheus with art, desire, descent and creation, death and rebirth, metamorphosis. Desire for the dead Eurydice fuels Orpheus's use of his art to create a bridge to the underworld. Orpheus descends to Eurydice by the power of his song, ascending to the surface only to lose his retrieved bride as the result of a premature backward glance. Alternating mythic versions conclude the Orphic journey with variations involving Orpheus's dismemberment by the Bacchae and the retrieval of his transfigured head, which becomes oracular. While his dismemberment and post-descent transformation link Orpheus to metamorphosis, this stage of his journey is not the one for which Orpheus is primarily known. Orpheus, as a hero and an artist, a triumphant and a tragic figure, is famous for the transcendence of human limitations inherent in his descent into the Underworld. Interpretive approaches to Orphic myth have evolved through various generations. Like modern existence, Orphic myth is fraught with paradox: the Orphic dilemma—to view the unknown is to lose the unknown, its mystery extinguished—is very similar to the modern experience, and its shattering of traditional belief systems, the triumph of science over mystery, the loss of the exotic in the wake of exploration and imperialism. Relevant to the modern audience and artist is Orpheus's descent into death, the chaos of the unknown, and his return by the power of his art.

Maurice Blanchot's essay "The Gaze of Orpheus" interprets the Greek myth as a psychological metaphor for creation, emphasizing that a work cannot be created unless the artist descends. The artist must "pursue the enormous experience of the depths—an experience which the Greeks recognized as necessary to the work, an experience in which the work is put to the test by that enormousness—...for its own sake" (Blanchot, 99). Blanchot relates this descent to the
existential quest of facing the other in one’s self and emerging thus transformed. Orpheus emerges from Hades, having met the forbidden gaze of his dead bride, and facing what Blanchot terms his death in death (his own extinction) he returns with this knowledge, either destroyed or renewed by it. Conrad’s concept of the modern artist incorporates this archetype of Orphic descent and renewal. Marlow experiences the enormousness of the depths and faces himself as other(s) throughout the Marlovian tales—notably through Jim, Stein and Brown, in Lord Jim. The idea of Orphic descent is more historically elaborated on in Walter Strauss’s Descent and Return: the Orphic Theme in Modern Literature, which traces three stages in the development of the Orpheus myth: (1) the sixth century B.C. Hellenistic cult; (2) the Renaissance Orphic archetype of the poet based on Virgil and Ovid; and (3) the modern concept of Orpheus, where he functions as the emblem of metamorphosis, the embodiment of transformation. Appealing especially to the conflicting values of the modern age, Orpheus is, for Strauss, the meeting point of the Apollonian and the Dionysiac (Strauss, 6-7), and the link between the Romantic and the modern. While Strauss never mentions Conrad, his explanation of Orphic appeal to modern writers certainly pertains to the author of Lord Jim. As the link between the Romantic and the modern, Orpheus serves Conrad’s modern and Marlovian purposes.

Strauss cites Mircea Eliade as best expressing the particularities of Orphic myth which “make it eminently suitable to a certain kind of modern mentality” (Strauss, 5) and which thus make it suitable for Conrad. In Images and Symbols: Studies in Religious Symbolism, Eliade explains how Orphic myth lingers in the matrices of the modern imagination:

The life of modern man is swarming with half-forgotten myths, decaying hierophanies and secularized symbols. The progressive desacralization of modern man has altered the content of his spiritual life without breaking the matrices of his imagination: a quantity of mythological litter still lingers in the ill-controlled zones of the mind. (Eliade, 18)

Eliade’s “ill-controlled zones of the mind” recall the subconscious realm in which the Conradian artist descends to make his appeal in the Preface to Nigger. The heap of mythological waste
products in Lord Jim includes the Christian imagery associated with Jim and the Orphic descents associated with both Jim and Marlow. Strauss evokes Conrad’s modern mythmaking when he describes modern mythopoeia as a “private fabrication utilizing traditional personae and details...to protect a personal vision of the world that expresses a certain notion about man and his ‘reality,’ the world, and some power or destiny that lies beyond or within” (Strauss, 4). As a symbol of transformation and reconciliation of opposites, Orpheus provides the opportunity to redefine modern values, including the destiny of “the poet and poetry” (Strauss, 9). Through his metamorphic night journey, Conrad’s Orphic artist Marlow links the Romantics Stein and Jim to the modern world and establishes the artist as the prophet, priest, or divinity of the modern age.

The Orphic artist always descends to Eurydice and all of Conrad’s artists in Lord Jim have a corresponding figure of Eurydice: Stein’s Eastern bride, the princess, dies in Patusan; Brierly’s bride, like Jim’s, is a Romantic vision of himself; Brown’s stolen bride languishes of a fever as does Stein’s. For Marlow, Eurydice is embodied both by Jim and Jewel. Jim’s Eastern bride—vital to his Orphic identity—is not really developed in the novel until Marlow becomes active in deciding Jim’s fate. Jim’s Romantic dreams and missed chances for heroism are mentioned, but they do not take on a (female) body until he meets Marlow in the Malabar House.

Jim’s Eastern bride has her roots in his Romantic dreams, the objects of his desire, “the best parts of his life, its secret truth, its hidden reality” (13). Jim “loved these dreams and the success of his imaginary achievements” (13), and it is to these dreams that Jim refers in the Malabar House when he mourns the “chance missed” (51) to realize such “Romantic achievements” (51) through heroism aboard the Patna. Jim’s imaginary achievements possess a (manly) “tread” before they are provided with a (female) body: “They had a gorgeous virility, the charm of vagueness, they passed before him with an heroic tread” (13). Marlow initially indicates Jim’s Eastern bride as a nebulous form: “a vague white form erect in the shadow, that, being looked at, cringed forward, hesitated, backed away silently” (71). The first explicit reference by Marlow to Jim’s dream or opportunity as embodied in an Eastern bride occurs as Jim’s dug-out enters
Patusan: “And his opportunity sat veiled by his side like an Eastern bride waiting to be uncovered by the hand of the master” (149). Marlow follows this statement by declaring Jim “the heir of a shadowy and mighty tradition!” (149). The appearance of Jim’s Eastern bride immediately provokes Marlow into identifying Jim as the heir of a tradition—the “shadowy and mighty” tradition, we might suggest, of the Romantic.

References to his Eastern bride are most numerous in Patusan, where Jim briefly realizes his Romantic dreams. Marlow describes this bride as again by Jim’s side when Jim makes the series of leaps or descents in Patusan that free him from the Rajah’s stockade to ally himself with Doramin. Jim emerges from the mud reborn as a heroic figure rather than as an exile cheated by fate, “and the opportunity ran by his side, leaped over the gap, floundered in the mud...still veiled” (154). When Marlow sees Jim for the last time alive in Patusan, Jim is Lordly, “white form head to foot...persistently visible with the stronghold of the night at his back, the sea at his feet, the opportunity by his side—still veiled” (204). Marlow questions if, since Jim seems to have been redeemed in Patusan, the opportunity is still veiled, but he is unable to answer his own question: Jim remains located “at the heart of a vast enigma.” The final allusion to Jim’s Eastern bride corresponds with Jim’s death: “For it may very well be that in the short moment of his last proud unflinching glance, he had beheld the face of that opportunity which, like an Eastern bride, had come veiled to his side” (253). Again, Marlow is not certain if that opportunity has truly been realized, if Jim’s death is a heroic act and his final redemption or only a final meaningless act of destruction—“whether his line of conduct amounted to shirking his ghost or to facing him out” (119).

Jim has his Eurydice, then, but his overall imperceptibility adds an element of Eurydice to his own character, at least for Marlow; Marlow’s own Orphic function is suggested by his many references to Jim’s veiledness or obscurity. In describing his last view of Jim as he departs Patusan, Marlow portrays the younger man as both Christ-like and Orphic, but also in Eurydice-like terms as a figure who is lost at the very moment he (like she) is seen:
He was white from head to foot, and remained persistently visible with the stronghold of
the night at his back, the sea at his feet, the opportunity by his side—still veiled. What do
you say? Was it still veiled? I don’t know. For me that white figure in the stillness of
coast and sea seemed to stand at the heart of a vast enigma. The twilight was ebbing fast
from the sky above his head, the strip of sand had sunk already under his feet, he himself
appeared no bigger than a child—then only a speck, a tiny white speck, that seemed to
catch all the light left in a darkened world… And, suddenly, I lost him…. (204)

Though recalled above in terms that evoke the Christ child, Jim is here also an obscured
Eurydice. Jim, as usual, vanishes. Marlow’s dilemma is the Orphic dilemma. Close scrutiny leads
to the loss of the subject he has repeatedly resurrected.

In telling Jim’s tale, Marlow contemplates how Jim would tell it. Implicit in his thoughts on
Jim’s telling is the idea that Jim would not lift the veil or offer any real clarity or “orientation” to
his identity either:

I wonder how he would have related it himself. He has confided so much in me that at
times it seems as though he must come in presently and tell the story in his own words, in
his careless yet feeling voice, with his off-hand manner, a little puzzled, a little bothered,
a little hurt, but now and then by a word or a phrase giving one of these glimpses of his
very own self that were never any good for purposes of orientation. (208-209)

Marlow’s words intimate that Jim could rise again at any moment. Just as Marlow’s narrative
offers no clear and final truth, neither does Jim’s narrative, which also veils him. Marlow’s
perpetual representation of Jim’s imperceptibility evokes the forbidden gaze of Orpheus at
Eurydice. Like Orpheus, Marlow is not truly supposed to see Eurydice as he ascends from the
underworld. Eurydice is the other, the unknown, the mystery. Marlow tells his audience, “Neither
you nor I will ever look like this on any man” (52), suggesting modern isolation and Jim’s
individual inscrutability in his function as the embodiment of the mystery behind the veil of the
visible world. Marlow’s statement that “to watch his [Jim’s] face was like watching a darkening
sky before a clap of thunder, shade upon shade imperceptibly coming on, the gloom growing mysteriously intense" (44) demonstrates how Jim’s obscurity increases in proportion to Marlow’s scrutiny.

Another of Marlow’s comments on Jim’s inscrutability reiterates the idea of the lack of “orientation” provided by Jim himself and compares Jim to an unexplored country. Marlow subtly links Jim’s identity to that of (what we will be arguing is) the Romantic construction of feminized Patusan:

I don’t pretend I understood him. The views he let me have of himself were like rents in a thick fog—bits of vivid and vanishing detail, giving no connected idea of the general aspect of a country. They fed one’s curiosity without satisfying it; they were no good for purposes of orientation. Upon the whole he was misleading. (47)

Underlying Marlow’s confusion concerning Jim’s nature and Jim’s imperceptibility is the latter’s own lack of self-knowledge; ironic in Marlow’s confusion concerning Jim’s nature is Marlow’s lack of self-knowledge. Jim is the feminized unexplored country of Marlow’s past or inner self. While Marlow affirms that Jim “would appear to my staring eyes distinct of form and pregnant with appeal like a symbolic figure in a picture” (81), Marlow fails to define Jim’s appeal or Jim’s meaning as his own alter-ego: “He was not—if I may say so—clear to me. He was not clear. And there was a suspicion he was not clear to himself either” (107). Marlow’s fear is Orpheus’s dilemma: “it was the fear of losing him...for it was borne upon me suddenly and with unaccountable force that should I let him slip away into the darkness I would never forgive myself” (109). Like ghostly Eurydice, Jim “kept his distance” (53); Jim is the aspect of himself that Marlow cannot see, or can only see at the cost of losing it once and for all.

Orphic Marlow effectively begins to lose Jim the moment his gaze meets Jim’s at the inquiry. Jim eventually does slip away into the darkness of his own final death; he is permanently fixed in the underworld of Patusan by the gaze of Doramin’s pistol barrels. Marlow fails to resurrect Jim, though he does summon Jim’s ghost, as he himself comments, through the Orphic weaving of his
tale. Telling Stein about Jim, Marlow notices, “At that moment it was difficult to believe in Jim’s existence…but his imperishable reality came to me with an irresistible force” (132). Marlow pursues Jim’s ghost into Patusan, perpetually increasing the concentration of his scrutiny until he loses Jim twice over—he sees what Maurice Blanchot would term Jim’s death in death. Marlow may ascend from Patusan/Hades, but he is forever locked in his own text, in the creation of and the loss/destruction of Jim—in the Orphic dilemma. That there is a mystery behind the veil of the visible world can be represented by Jim and communicated by Marlow, but the mystery itself is inexplicable despite Marlow’s scrutiny.

The reciprocal gaze, a recurrent motif in Lord Jim and integral to the myth of Orpheus and Eurydice, perpetuates the enigma at the heart of Lord Jim. Jim meets Marlow’s gaze at the inquiry, the French Lieutenant pierces Marlow’s gaze in the café, Dain Warris’s eyes are fixed in a death gaze, the fierce gaze of the dying Brown compels Marlow to listen, Jewel’s dark eyes demand an answer, Stein’s perceptive gaze echoes Doramin’s pistol barrels, and Doramin’s final deadly gaze concludes Jim’s life. Allon White, in The Uses of Obscurity, identifies Conrad’s use of the gaze as another mechanism adopted to render the mystery behind the veil enigmatic, “endlessly reflective” (116). In Conrad’s works, the gaze is an inversion that results in the transference from subject to object and “the discursive production of ‘mystery’ by the mirror process” (White, 116). Conrad’s characters look (pun intended) to each other for answers but see only more questions. According to White, Conrad’s motif of the gaze is characteristically feminine, effecting “the specular equivalent of narrative suspension” (117), and making the reader feel “that there is something to be expressed other than that which objectively offers itself to expression” (White, 118). That something implied but not expressed is the enigma.

Facing the enigma and experiencing descent are integral in Conrad’s artistic manifesto as expressed in his Preface to Nigger, and it is the combination of recurring gazes and descents that first linked Blanchot’s “Gaze of Orpheus” with Lord Jim in my mind. The multiple descents and reciprocated gazes in Lord Jim reflect the reader’s attention back to the artist. This reflection has
a narcissistic dimension. Conrad’s use of Orphic, Christian, and other mythic elements in Lord Jim has the effect of valorizing the artist, his descents, his gaze, his textual doubles; in his exploration of the power of the artist, Conrad exhibits a “modern self-consciousness” (Strauss, 11) that narcissistically sacralizes the figure of the artist. Nowhere is this narcissism more apparent in Lord Jim than in Jim’s relation with his “Echo,” Jewel, the novel’s primary feminine principle.
(iii) Myth and the Feminine Principle: Jewel

One of Jim’s Eastern brides is Jewel, the most disturbing character in Lord Jim. Jewel’s grief disturbs Marlow, Stein and the reader by calling Jim’s trueness into question. As the only real woman in the novel and featured in the feminine landscape of Patusan, Jewel is one of the most complex symbols in Lord Jim. Jewel reinforces the links between the doubled Romantic heroes in the novel by invoking various mythic females and tragic female figures at once. Yet another ill-fated bride, Jewel connects Jim with alter ego Brown by recalling Brown’s doomed lover, and she associates Jim with Romantic double Stein by recalling Stein’s dead wife and child. Jewel’s tragic figure eerily doubles Jim, and because both function as a type of Eurydice, both evoke the inexplicability of the mystery behind the veil of existence. Jewel simultaneously embodies and rejects the motif of Jim’s veiled Eastern bride, just as she violently rejects Jim’s Romantic self-sacrifice at the novel’s end.

Jewel evokes the three dead women already entombed in Patusan—the princess, Emma, and Jewel’s mother. These three women prefigure Jewel’s destiny, hovering in the background like three fates. Jewel is trapped in the Underworld of Patusan, like her mother before her, tormented by Cornelius, and then abandoned by Jim. Approaching Jewel’s mother’s grave, Marlow describes the mother’s fate in a vision which forebodes her daughter’s own fate: “there is visible in its background the melancholy figure of a woman, the shadow of a cruel wisdom buried in a lonely grave, looking on wistfully, helplessly, with sealed lips” (168). The two women blur together, suffering the same fate. Marlow “can not help picturing...first the young woman and the child, then the old woman and the young girl, the aweful sameness and the swift passage of time” (169). Even Cornelius links the two women: “Like her mother—she is like her deceitful mother. Exactly. In her face, too” (200). Jewel’s ghostly existence in Stein’s catacomb-like household
following Jim’s death reiterates her connection to these entombed or doomed women. Something eerily redolent of the demon-lover hovers over the tragic fate of Brown’s lover, Stein’s wife, Jewel’s mother, and Jewel. Instead of fertility in the union of man and woman in Lord Jim, there is a pattern of dead or abandoned muses in the wakes of Conrad’s Romantic heroes that cannot help but evoke Eurydice.

Jewel plays a part in the supernatural legends that spread about Tuan Jim in Patusan and magnifies the Romantic idealism of Patusan by doubling Jim. Jewel’s name “means precious, in the sense of a precious gem” (169); Jewel jealously guards her precious Jim (pun intended). This pun on their names (gem/Jim) reinforces their relationship as doubles. Jewel and Jim greet each other as “boy” and “girl” (195), indicating their archetypal roles as the mythic hero and the mythic heroine in Marlow’s framing of their story: “they came together under the shadow of a life’s disaster, like a knight and maiden meeting to exchange vows amongst haunted ruins” (189). Jim describes finding Jewel as one might “go out on a stroll and come suddenly upon somebody drowning in a lonely, dark place” (185). After Jim rescues Jewel, they are “two white forms, very close...[whose]...soft murmurs reached...[Marlow]...penetrating, tender...like self-communion of one being carried on in two tones” (173). They double each other in their white imagery and inscrutability, and create a new harmony in Patusan; yet, Jim ultimately chooses, like Narcissus, the Romantic image of himself over the realized self Jewel offers him and Jewel is left “soundless, inert” (253)—a used up Echo.

Jewel’s relationship with Jim lends her a richly mythic air, evoking a plethora of female archetypes at once. Just as Jim is both Orpheus and Christ, Jewell is both Eurydice and more, paradoxically recalling Eve and the Madonna as well. “With her head fallen back[,] her hair touch[ing] the ground” (251), Jewel is most Eve-like. When she saves Jim’s life and mourns his loss, she evokes the Madonna. One night Jewel emerges half-seen, veiled by the darkness, to wake Jim and warn him of the imminent attempt on his life. Jewel attempts to save Jim from death again at the novel’s end by reminding him of his vow to her. Robert Andreach and Joseph
Campbell assert that by providing the hero with supernatural aid, the mythic woman protects his quest, "a figure of the Virgin Mary, mother of Redemption and Mediatrix of grace" (Andreach, 22). Jewel’s ultimate grief is also similar to that of the Madonna who bears a son only to lose him as a sacrifice to mankind. Jim’s frequent comparisons to Christ reinforce Jewel’s connection to the Madonna, again indicating the dysfunction of Christian redemption. Marlow’s descriptions of Jewel emphasize her whiteness: he perceives her “white figure ...shaped of snow; the pendant crystals of a great chandelier...above her head like glittering icicles” (211). Not only does Jewel’s whiteness evoke the purity of the Madonna and of virginal Eurydice or Persephone (the latter two also trapped prematurely in the Underworld), her whiteness also signifies the enigmatic whiteness of the abyss (which was evident to Jim after his leap into the Patna lifeboat).

Allon White’s “Joseph Conrad and the Rhetoric of Enigma” in his Uses of Obscurity discusses the use of whiteness in Conrad’s works to denote absence or blankness that signals the position of a secret to be discovered; according to White, whiteness signifies enigma. White’s explanation of how Conrad’s rhetoric of enigma feminizes the incomprehensible explains the doubling of the real woman, Jewel, and Jim, feminized by his white attire and his inscrutability:

His rhetoric of mystery is omnivorous. ‘Woman’, ‘unconscious’, ‘nature’, ‘language’, these are effectively placed into a single paradigmatic set by their common designation as ‘enigma’. They are all rewritten ‘like a script in an unknown language’, and this has the crucial consequence that they are symbolically interchangeable on the basis of their resistant incomprehensibility. (118)

Both Jim and Jewel embody the subconscious need for wonder and both function to mirror the mystery behind the veil of the visible world. That Jim does not recognize Jewel as part of himself or as the embodiment of mystery is part and parcel of her inscrutability and of his own lack of self-knowledge. When Jewel laments to Marlow, "He went away from me as if I had been worse than death. He fled as if driven by some accursed thing he had seen or heard in his sleep" (212), she reinforces her link with the subconscious and the disparity between the subconscious dream
Jim might have followed and the one he chooses. Jewel’s comment also reiterates Jim’s identification with Brown, desperately fleeing the specter of a prison.

While Jim is the one who leaves Jewel behind, Marlow is the artist who recognizes in Jewel the inscrutable mystery of Eurydice. Marlow comments again and again on Jewel’s inscrutability. While Marlow never connects this inscrutability to Jim’s, the phrases he uses to describe the two are so similar that Jewel effectively seems as veiled, obscure and ghost-like as Jim. Marlow first encounters Jewel in the dark, and all he can see are “the flowing lines of her gown, the pale, small oval of her face, with the white flash of her teeth, and...the big, sombre orbits of her eyes” (187). Marlow’s descriptions of Jewel’s eyes suggest the function of her gaze as similar to that of Blanchot’s mysterious other. Jewel’s eyes remind Marlow of “an immensely deep well.” To Marlow, Jewel is “more inscrutable in her childish ignorance than the Sphinx propounding childish riddles to wayfarers” (187). Jewel makes a nameless demand on Marlow: “She wanted an assurance, a statement, a promise, an explanation...—the thing has no name” (186). Marlow describes how “it was impossible to distinguish her features, the darkness of the eyes was unfathomable; two wide sleeves uprose in the dark like unfolding wings, and she stood silent” (187-188), a mourning Madonna, an inscrutable Eurydice. Marlow looks at the stream beside Jewel, which rolls “silent and as black as the river Styx” (190), and feels somehow responsible for her, as an Orphic artist should. Jewel tells Marlow, “in a voice as quiet in the obscurity as her white [my italics] half-lost figure,” that she wants Jim to save her from her mother’s fate, that she does not want “‘to die weeping’” (190), abandoned and buried in the underworld of Patusan.

Marlow can neither comfort Jewel nor save her—her mythic role is to be inscrutable and to be left behind and Marlow’s role is to ascend from the world in which he leaves her behind (which, of course, provides fuel for thought for a feminist criticism of Conrad’s aesthetics in this novel!):

‘She said we lied. Poor soul! Well—let’s leave it to Chance, whose ally is Time, that cannot be hurried, and whose enemy is Death, that will not wait. I had retreated—a little cowed, I must own.... I had only succeeded in adding to her anguish the hint of some
mysterious collusion, of an inexplicable and incomprehensible conspiracy to keep her forever in the dark.’ (195)

With this unintentional lie (reminiscent of the one he tells Kurtz’s Intended at the end of *Heart of Darkness*) Marlow assumes the role of spokesperson for all Orphic artists, addressing the woman—and the mystery—that is always left behind. Jewel certainly foretells her own fate when she doesn’t believe Jim’s promise and tells Marlow, “Other men had sworn the same thing” (191). Her father left her mother, and her mother’s father had left her mother, too. Marlow certainly cannot aid Jewel; her protests only reiterate the futility of protest.

In addition to directing the reader’s attention to the issues surrounding Jim’s heroism, Jewel’s inconsolable grief also directs the reader’s attention to the significance of Marlow’s heroism. Just as it is Jewel’s role never to leave the underworld, it is Marlow’s Orphic role to ascend. Marlow’s visit to Jewel at Stein’s marks the point in the novel from which he can begin his ascent, and break from the underworld in which Stein and Jewel will remain. After Jim’s death, Jewel leads “a sort of soundless, inert life in Stein’s house” (253), and Marlow, attempting to console her, is surprised “to discover that she had a voice at all” (192). Marlow describes Jewel as “a poor mortal [like Jim] seduced by the charm of an apparition...[trying] to wring from another ghost the tremendous secret of the claim the other world holds over a disembodied soul astray amongst the passions of this earth” (192). It is unclear if the ghost she attempts to wring the secret from is Marlow or Jim. Marlow’s remark—“Her immobility before me was clearly expectant, and my part was to speak for my brother [Jim] from the realm of forgetful shades” (192)—briefly locates him in the realm of the shades along with Jim. Marlow “would have given anything for the power to soothe her frail soul, tormenting itself” (192), but he cannot soothe Jewel’s soul. Unlike Jim, when Marlow turns from Jewel, she propels him forward in his mythic journey to emerge from the underworld of Patusan (or Stein’s home) with his identity as an artist and his tale of descent intact.
As Andreach argues, “Of the three men who travel up an S-shaped river into the heart of darkness—Kurtz, Jim, and Marlow—two straggle and die whereas the third is reborn” (62). Andreach asserts that Jim “becomes the slain god by fleeing from [Jewel]” (Andreach 63), and that “demanding redemption on his own terms” (Andreach, 61) is a form of betrayal and no true redemption at all. Jewel is Jim’s guide to survival in Patusan. In preventing his early assassination and offering him a choice he realizes that he cannot make, Jewel extends Jim’s opportunity for self-discovery. Jim accepts Jewel’s guidance on matters in Patusan, especially during the night of his attempted assassination; but he will not allow her to guide him out of Patusan, away from his idealistic but outmoded code of honor, or to the self-knowledge that would allow him to reject this code. Unlike Andreach, I argue that Jim cannot accept Jewel’s demand because Jewel can offer Jim no redemption. Jewel never believes in Jim’s dishonor; she cannot offer Jim any true sense of redemption because she does not believe he has fallen. As a Romantic hero, Jim must turn away from the real woman, and act individually. Jim sees Jewel as a real woman; Marlow sees Jewel as the embodiment of mystery. The sterility of Jim’s isolation also reflects the sterility of modern isolation: Jim must make his own meaning, in the absence of others. Defining redemption in his own terms is also something a modern hero must do. Jim defines it in Christ-like gestures, as the son of a minister might be expected to do.

Refusing to humble himself before the unknown and before the unknown mystery of the heroine, according to Andreach, has dire consequences for the hero:

The heroine is the catalyst for...self-discovery: if he does not reject her, she will guide him to the region of supernatural wonder within himself. This initiation is his religious experience. The male who persists in his illusion that he does not have anything in common with the rest of mankind does not redeem himself because he does not have the experience that makes the moral response possible. Refusing to humble himself before the mystery in her person, he misses the opportunity to humble himself before his own mystery, which would be an acknowledgement of his kinship with all of mankind and the
beginning of a moral response. By invading her or by ignoring her reality, he finds what
he is fleeing, death, since he does not realize himself as a human being in moral action.
(Andreach, 57-58)

According to Andreach, instead of being humble before feminized Patusan or Jewel, Jim is
hubristic and amoral, as is evidenced in the following passage: "'Nothing can touch me,' he said
in a last flicker of superb egoism" (251). He refuses to have anything in common with the other
officers of the *Patna* or with any other character besides Stein and Marlow. Neither Stein nor
Marlow seem amoral, however; and neither Stein nor Marlow fully condemn Jim. Saying
goodbye to Marlow and refusing to leave Patusan does not necessarily sever Jim’s last link to the
world outside Patusan, as Andreach argues. Andreach’s analysis explores descent in Christian
rather than Orphic terms. Conrad’s theme is solidarity, his primary archetype for the artist is
Orphic, and Marlow is determined that Jim is one of us: Marlow is Jim’s tenuous Orphic link to
humanity. Orphic Marlow can briefly resurrect Jim and Jewel with each telling of his tale, and
with each telling he is “touched” (as will be the reader) by the Romantic wonder of Jim and by
the anguished wisdom of Jewel—figures of ancient mythologies rewoven to suit Conrad’s
attempts at reimposing a vision of artistic order on the chaos of the modern world.
(iv) Conrad's Impressionism: Involving the Reader in Myth-Making

Literary impressionism depicts a scene or character through details "intended to achieve a vividness or effectiveness more by evoking subjective and sensory impressions than by recreating or representing an objective reality" (Merriam-Webster, 583). The impressionist—Conrad in this case—aims "to achieve a fuller truth than realism can," by evoking in the reader an "intricate play of emotion ... a rich conflict of sympathy and judgement, a provisional bafflement in the face of experience" (Guerard, 390). One of Conrad's most astute critics, Ian Watt, has discussed how Conrad's impressionism results from, and relies on, his shift to Marlow's first person disjointed narrative chronology a few chapters into the novel, and the interposing of scenes and doubling of characters that results from this shift, and which establishes an ambiguous emotional interplay in the reader by depicting the fuller truth of experience that cannot be represented by the realist novelist. I argue that the disparate mythic and supernatural allusions and ritual elements of Lord Jim that form the mythic substructure of the text are also part of Conrad's impressionism; their association with the novel's primary artists lends the concept of artistry a mythic religiosity. Conrad's mythic substructure is yet another of his impressionistic devices used to communicate man's dependence on a community of men to interpret reality and the interdependence of the artist and the audience in defining meaning and creating a new mythology.

Conrad's impressionism begins on the title page of Lord Jim with a quote from the German Romantic Novalis that evokes the dynamics of confession. Confession, another impressionist device, which I discuss near the end of this thesis, is a recurrent motif in the novel. The opening line from Novalis further sacralizes the role of the artist and points to the human need for solidarity: "It is certain my conviction gains infinitely the moment another soul will believe in it."
Strauss indicates that Novalis was intoxicated with mythological and symbolic thinking. Novalis used Orpheus as a bridge between body and spirit. Conrad's referencing of Novalis, whose Dantean poem *Hymns to the Night* involves artistic descent to his beloved Sophie, reinforces Conrad's theme of descent and invokes the psychological doubling, the politics of confession, and the impressionism employed throughout the mythic substructure of the novel.

As anticipated through the Novalis epigraph, the narrative frame of *Lord Jim* establishes a situation in which both the reader and the narrator's audience are invited to see Jim and Marlow as psychological doubles of themselves enacting mankind's subconscious needs for wonder and for interdependence. Jim enacts exalted egoism; Marlow sees in Jim a younger version of himself and relates to and comments on Jim's egoism time and again. The interdependence of the two characters, confessor and confesser, at once represents mankind's need for interdependence and the interdependence of the hero and the artist in literature and in society. Of course, the reader and audience only experience the dynamics of Marlow's confessional relationship with Jim through Marlow's vacillating narrative, which itself becomes an ambivalent form of confession directed at them.

As first person narrator and Conrad's primary impressionistic mechanism, Marlow alternately empathizes with Jim's youth and then criticizes Jim's egoism. Marlow beholds Jim at the inquiry and responds to Jim's uncertain fate with a feeling of unavoidable solidarity, which Marlow, in turn, conveys to the reader. At times, Marlow is disgusted by Jim's egoism; at others, he is touched by Jim's anguish or admires Jim's determination to face the inquiry. Marlow outlines Jim's desperate eastward trek with parental concern and frustration and traces Jim's later rise and fall in Patusan with a suggestion of parental pride and grief. Incidents or comments condemning Jim interrupt passages in which Marlow is sympathetic to the young man. Scenes and doubled characters are thematically overlapped in order to manipulate the reader's judgment towards an ambivalent response to Jim's egoism (something that the omniscient and straightforward narrator of the novel's opening chapters could not achieve).
Ultimately, in recounting Jim’s death, Marlow neither condemns nor condones Jim’s actions. Conrad concludes Lord Jim with Marlow’s critical comments on Jim’s abandonment of Jewel—”He goes away from a living woman to celebrate a pitiless wedding with a shadowy ideal of conduct” (253)—and with Marlow’s comments about Jim’s inscrutability. Marlow confirms his own confusion by questioning his own judgment and involvement in Jim’s affairs: “Was I so very wrong after all?” (253). With this rhetorical question and a wave from the dying Stein, Marlow’s tale ends with no easy answer to the inefficacy of Jim’s function as a hero or as an artist. While the opening Novalis epigraph invites the reader to share Marlow’s conviction, Marlow often seems to lack conviction. Jim’s conflicting shame and determination, his Lordly conduct in Patusan and then Jewel’s condemning grief, further complicate Jim’s character as well as the reader’s response to it. Because of the resulting “provisional bafflement,” the reader is not certain how to judge Jim’s egoism; Marlow’s, and therefore the reader’s, lone firm conviction—or truth—is that Jim “is one of us” (253). Included in that “us,” readers must question the values defining their world and answer these questions for themselves, by considering the stories of Conrad’s doubled heroes and artists interposed throughout Marlow’s narrative, as well as the subjective utterances of which (and with which) those stories are made up.

In addition to Marlow’s ambivalent opinion of Jim, each interposed passage and each doubled character reveal a disparate perspective or fragment of truth concerning the complex issue of Jim’s dilemma and destiny. Conrad considered it the writer’s ethical “task to rescue ‘the image of truth’ from the flux of reality, thereby communicating to the reader a sense of human continuity and fellowship” (Fraser, 5-6). Another important passage from his Preface to the Nigger of the ‘Narcissus’ describes this sacred task of the artist:

The task approached in tenderness and faith is to hold up unquestioningly...the rescued fragment before all eyes in the light of a sincere mood. It is to show its vibration, its colour, its form; and through its movement, its form, and its colour, reveal the substance of its truth.... In a single-minded attempt of that kind, if one
be deserving and fortunate, one may perchance attain to such clearness of sincerity that at last the presented vision of regret, of terror or mirth, shall awaken in the hearts of the beholders that feeling of unavoidable solidarity; of solidarity in mysterious origin, in toil, in joy, in hope, in uncertain fate, which binds men to each other and all mankind to the visible world. (Conrad, Prefaces, x)

One ultimate, unified truth is beyond grasping or communicating, but fragments may be rescued. The fragments of truth rescued from the flux of reality through the doubled heroes and artists of Lord Jim indicate human social, psychological, and philosophical interdependence. While Conrad’s impressionism calls Jim’s heroism into question, neither Jim’s single-minded attempt to achieve heroism, nor his bond with Marlow, nor his link to the other doubles is ever questioned (despite what Andreach argues concerning Jim’s ultimate separation from humanity). Certainly, regardless of Jim’s cowardice or heroism, the respective bonds between Jim and Marlow, Jim and Stein, and Jim and Jewel survive Jim’s death. In his quest to realize his Romantic image of himself, Jim is as sincere as Marlow/Conrad is in his efforts at holding Jim up unquestioningly as a fragment of truth representing the conflicting values of the modern world. Jim is not the perfect hero, man, or god. His failings and successes and questionable ending reflect the “regret,” the “terror,” and the “mirth” of the “uncertain fate, which binds men to each other,” and which binds together Conrad’s character doubles.

Doubled characters such as Jewel, Marlow, Brierly, Stanton, the French Lieutenant, Brown, and Stein—all characters who tell a tale, descend, or are buried with mythic undertones—either call Jim’s heroism into question or confirm it. The responses of various character doubles to Jim affirm man’s need to define himself in a social context as a result of the “preoccupation and hesitations and audacities of modern thinking” (Strauss, 18). Jim, Marlow, Conrad, and his modern reader have “questioned the nature of reality, the nature of being, the nature of God, the nature of nature, and the nature of poetry and thought themselves” (Strauss, 18). Sorting through Marlow’s array of rescued truths, Conrad’s reader must recognize the inefficacy of traditional
values and Christian mythology in resolving either Jim's or the modern dilemma. "By taking us from a moribund tradition to a realm of archetypes to a re-created myth" (Andreach, 218), Conrad attempts to "redefine Western man's values and virtues to make them meaningful today." In the end, the reader emerges from the underworld with Marlow, who has—through the weaving of his tale/text—rewoven these fragments of truth and dead mythologies into a modern mythology. This modern mythology, like all of the older paradigms, involves a quest—indeed, several quests.
(v) **Quests in Progress: The *Patna* Episode**

*Lord Jim* begins in medias res, with two quests in progress: Jim has already descended, or leaped, from the *Patna* into his night journey and Marlow’s quest is also in progress, though he will not be introduced until the inquiry. In the process of moving east, Jim has already endured the inquiry, has already consulted with Marlow, and has already caused Marlow, too, to question the values defining his existence. Because the opening paragraph of *Lord Jim* takes the reader immediately into the underworld to face Conrad’s Romantic hero before Marlow ever appears, the mystery surrounding Jim is magnified. In the opening lines of the novel, a mysterious image of Jim advances towards the reader (indicated by the second person “you”) with “a fixed from under stare which made you think of a charging bull” (3). Conrad’s initial unidentified narrator provides this image, the “most concrete portrait of Jim we ever receive” (Lynn, 29), and immediately draws the reader into a head-on collision with Jim as he flees from what the reader does not yet know is the dishonor of the *Patna*. Because this initial unidentified narrator “shares the same moral foundation as Jim” (Lynn, 29), locating the reader here in Jim’s confused flight establishes the context of Jim’s unheroic failure to adhere to the moral code of his society when he leaps from the *Patna*.

The initial setting of an obscure string of progressively Eastern ports where Jim works as an incognito water-clerk is already pervaded by the sense of doom redolent of the *Patna*. Every setting after the *Patna* assumes the latter’s underworldliness. David Lynn describes Jim’s initial movements eastward as the “purgatorial years” (Lynn, 29), similar to the initiation stage of the heroic quest as discussed by Andreach. Jim’s progress away from the West parallels a religious pilgrimage or spiritual journey, though he is “a seaman in exile from the sea” (4). The reader is,
as it were, already in Hades, on a similar quest, and moving East with Jim. The novel will end
with an image of Jim’s “last proud and unflinching glance” (253) at the easternmost point of his
journey, facing his death in Patusan. At the end of Jim’s pilgrimage, he finds his Eastern Bride in
his own death. These opening and closing images of Jim’s unflinching glance are crucial in the
impressionist maneuvers of Conrad as he first presents and then destroys a problematical hero and
artist on a problematical quest. Jim’s inaugural and ultimate gaze also invoke Conrad’s rhetoric of
enigma. Marlow’s uncertainty surrounding Jim’s final culpability implies that Marlow’s quest,
and that of the reader, is still in progress, will always be in progress. Facing Jim’s final
unflinching reciprocal gaze, the reader, through Conrad’s impressionism, is involved in the
production of mystery, in what White refers to as Conrad’s mirror-process.

Conrad’s initial narrator increases the mystique of the *Patna* catastrophe by passing over it and
moving (in chapter four) directly to Jim’s trial. This unidentified narrator regresses from the first
unflinching image of the adult Jim to boyhood Jim’s Romantic dreams of himself being “as
unflinching as a hero in a book” (5). Jim’s boyhood dreams are ill met by his less than heroic
hesitation aboard the training-ship; this failure is an early example of how “his imagination, the
very source of his heroic image … undoes him” (Lynn, 36). After his first few years at sea, Jim
finds himself recovering from a falling spar at an Eastern port and accepts the fateful berth as
chief mate of the *Patna*, where he continues to dream an heroic life for himself until the ship’s
mysterious collision with an unidentified object and his unheroic leap. During the trial, Marlow’s
gaze meets Jim’s and Marlow’s identification with the younger man—the mirror-process—
begins; he takes over as first-person narrator. The reader henceforth accompanies Marlow on his
quest to make meaning of Jim’s dilemma. In consequence, the reader’s quest to decipher the
meaning of Jim and Marlow’s disparate yet conflated spiritual journeys—as well as his own—
begins.

The subsequently fragmented story of the *Patna* and Jim’s first catastrophic failure to realize
his dream, is told in turns by Jim, the engineer, Marlow, the helmsmen, and the French
Lieutenant. As the truth emerges, truth becomes a more abstract and increasingly relative concept for all involved. The Patna—the pilgrim ship—carries the reader, Jim, and Marlow on a journey of redefinition—of heroism, artistry, and existence; it takes them, and us, through the death of old traditions and mythologies towards the formation of a new value system. The ageless pilgrim ship becomes fraught with mythic power of her own. The Patna is the first of a series of feminized underworlds through which Conrad’s impressionism carries the reader along with his heroes Marlow and Jim.

The Patna is introduced into Lord Jim by the unidentified initial narrator as a vessel “old as the hills” (9); the ship becomes increasingly ageless and supernatural as she proceeds on her “errand of faith” (10) to the spiritual center of the (Islamic) East (paradoxically, in a journey westward). The Patna carries “eight hundred pilgrims (more or less)... urged by faith and the hope of paradise” (9). The unidentified narrator of chapters one through four describes how the “pilgrim ship” (10) passes over a sea that remains “still, without a stir, without a ripple, without a wrinkle—viscous, stagnant, dead... with a slight hiss” (11). The ship becomes more spiritually evocative as she progresses over this dead sea and leaves “behind her a white ribbon of foam that vanished at once, like the phantom of a track drawn upon a lifeless sea by the phantom of a steamer” (11). Already the white wake of the Patna seems to erase her path rather than to mark it—there will be no turning back. Jim dreams his virile dreams on a ghost ship sailing the stagnant sea of a dead world.

The days pass, “disappearing one by one into the past as if falling into an abyss for ever open in the wake of the ship,” and the nights “descended on her like a benediction” (11). In this other world, this underworld, of the Patna “a marvelous stillness pervaded the world, and the stars, together with the serenity of their rays, seemed to shed upon the earth the assurance of everlasting serenity” (11). Jim basks in this security and serenity as he watches the eight hundred various souls of the pilgrims, “all equal before sleep, death’s brother” (12). The dead world with the living hero is reminiscent of the underworld of Conrad’s Nigger Preface in which the dead, the
living, and the unborn meet. "The rows of prone bodies" (12), including that of "a woman covered from head to foot, like a corpse, with a piece of white sheeting" (yet another invocation of feminized mystery), seem dead. In the stagnant stillness of the *Patna*, Jim awaits an opportunity for heroism but little expects one, and the reader awaits an explanation of Jim's exile.

Jim's vigil on the *Patna* is characterized by "the taut stillness of an unspeakable power that lies in wait" (159), similar to the stillness pervading Marlow's river in *Heart of Darkness*. In *Heart of Darkness*, Marlow describes this stillness as that "of an implacable force brooding over an inscrutable intention" (Conrad, *Heart*, 56). Deborah Guth relates this stillness to "the stillness that precedes creation...not that of a world at peace awaiting the magic call of life" (159), but one awaiting destruction. Similarly, Jim's world of unquestioned tradition and codes of honor is about to be destroyed, left behind for an unfamiliar and frighteningly meaningless universe void of communal codes of honor. The hell-like undertones of this meaningless universe become more apparent in the figures of Jim's fellow officers as the moment of Jim's fall draws nearer in the text.

Jim's underworldly fellow officers contrast strongly with his unrealized Romantic dreams and emphasize the hellishness of the *Patna*. The three officers evoke "the incarnation of everything vile and base that lurks in the world we love" (14). In this underworld of the *Patna*, there is a yet more subterranean level, inhabited by the second engineer, whose voice beckons from below deck: "'Hot is no name for it down below,' said a voice" (14). The corpulent German skipper and the skeletal second engineer become demonic foils in Pandemonium. The German skipper is "dull-eyed, malevolent, and of soft, fleshy curve" (15), and the second engineer is "lean, all hollows, with a long head bony like the head of an old horse, with sunken cheeks, with sunken temples, with an indifferent glazed glance of sunken eyes" (15). When the second engineer moves, "a skeleton seemed to sway loose in his clothes; his walk was mere wandering" (15). While "those men did not belong to the world of heroic adventure" (16), they certainly belong to the underworld represented by the *Patna*, "poised on the brow of yawning destruction" (17).
The security and peace of the voyage is broken when the *Patna* suffers a surreal collision with an unidentified object, perhaps (as Marlow later puts it) “a kind of maritime ghoul on the prowl to kill ships in the dark” (97). The initial narrator’s communication of the *Patna* incident ends with the moment of collision. Marlow’s disrupted narrative fills in the gap between the collision and the trial. Jim relates to Marlow in the Malabar House how, after ascertaining the damage, he knew “there must be a big hole below the water-line” (18), that the bulging bulkhead will not hold, and that the *Patna* will sink. Jim’s imagination paints a vivid picture of his inability to save the pilgrims and Jim enters a personal hell, which he describes in Chapter Four during his trial. On the deck of the *Patna*, Jim is trapped; there are “eight hundred people and seven boats” (53). He states, “I was angry, as though I had been trapped. I was trapped! The night was hot, too, I remember. Not a breath of air” (63). Jim almost seems to feel buried alive in the moments before he jumps from the *Patna*.

Describing the scene to Marlow in the Malabar House, Jim is still on the *Patna*, “looking at these recumbent bodies, a doomed man aware of his fate, surveying the silent company of the dead” (53). In the mythic underworld of the *Patna*, “there was no time. No time!” (53); the seas around the *Patna* are likewise “deadly still” (56). As Jim watches the other officers struggle with the lifeboat, he sees “a silent black squall” whose “shadow flies over the waters, and confounds sea and sky into one abyss of obscurity” (62). Before descending even further into this enigmatic obscurity by leaping from the *Patna*, Jim stumbles over the legs of a dead man; when he jumps, Jim lands in a lifeboat that is more like a coffin, taking Marlow and the reader with him. Describing the deadlock between himself and the other officers on the lifeboat, Jim states that, “We were like men walled up quick in a roomy grave” (74).

Jim refers to his escape from the *Patna* as “a joke hatched in hell” (66): it was “as if I had jumped into a well—into an everlasting deep hole...” (68), into which “the end of the world had come through a deluge in a pitchy blackness” (69). The rainy darkness of the lifeboat “was like being swept by a flood through a cavern” (69). In the darkness and silence of the lifeboat, the
officers can discern no sign of the *Patna* and can hear nothing. Jim says, "'You couldn't distinguish the sea from the sky; there was nothing to see and nothing to hear. Not a glimmer, not a shape, not a sound'" (70). The lifeboat becomes an abyss of "annihilation," in which "everything was gone and—all was over..." (70). Thus one world ends, and another begins, in an abyssal stillness: "only a night; only a silence" (70), "not a star, not a light anywhere" (72).

In her account of *Heart of Darkness*, Guth explains the nature of this abyssal experience: "From the point of view of the Quest myth," she asserts, it represents "one of the ordeals which the hero must overcome in order to reach his goal" (Guth, 160). From the perspective of the creation myth that Guth identifies as central to Conrad's earlier novella, Jim is in between worlds. His world has just been destroyed, returning him to a primordial past: "Within the explicit context of a return to the past, however, the sense of an ending is unmistakable" (Guth, 160). Jim's assumed but never challenged unity with society and Western tradition has ended: not only has he missed an opportunity for heroism, but he has acted the part of a scoundrel and will become a social pariah. From this point on, like Milton's Satan, Jim will carry his hell (his leap from the *Patna*) with him wherever he goes. For Jim, a world and all its communal creeds and their meaning have died. Marlow supports Jim's existential description of his experience on the lifeboat:

> There is something peculiar in a small boat upon the wide sea. Over the lives borne from under the shadow of death there seems to fall the shadow of madness. When your ship fails you, your whole world seems to fail you; the world that made you, restrained you, took care of you. It is as if the souls of men floating on an abyss and in touch with immensity had been set free for any excess of heroism, absurdity, or abomination. (74)

Marlow comments further on the isolation of Jim and the other officers in the lifeboat, cut off "more completely from the rest of mankind, whose ideal of conduct had never undergone the trial of a fiendish and appalling joke" (74). Marlow continues, "Trust a boat on the high seas to bring
out the Irrational that lurks at the bottom of every thought, sentiment, sensation, emotion” (74). As Guth's analysis indicates, the mythic creation/descent of the *Patna* codifies the irrational and the supernatural forces at work in Jim’s life. Marlow contributes to this codification by interposing the existence of “Dark Powers whose real terrors, always on the verge of triumph are perpetually foiled by the steadfastness of men” (74). Neither Jim nor his fellow officers have been steadfast; in this case, the Dark Powers have not been foiled. Marlow’s remarks reveal that both he and Jim are struggling artists, determined to make meaning out of the abyssal chaos that confronts them.

The morning after his dark six-hour vigil Jim watches the sea “giving birth to the globe of light,” which the reader realizes is the sun (75), but in effect Jim never emerges from the underworld of the pilgrim ship. This globe of light, the sun, that ironically appears in the midst of Jim’s darkness will later re-appear in the form of the globes of light in the Malabar House dining area, in the candles floating through the cavernous gloom of Stein’s home, and in the torch which Jewel flings into the river in Patusan. These lights mark either the destruction of the old world of traditional values and of the code of conduct defining honor and dishonor, or the birth of a new world—a modern world in which the values represented by this code are lost.

With the morning comes the sight of the other officers—a bizarre Trinity of “three dirty owls” (77)—and an abyss not of darkness this time but of light. Just as the complete and unbroken darkness of the night before had resisted Jim’s powers of perception, so does the unbroken whiteness of the new day. “It was dead calm,” and “all was light, light, and the boat seemed to be falling through it” (77). Both the whiteness—a crucial sign in Conrad’s rhetoric of enigma, as Allon White suggests—and the darkness are indecipherable. Traditional dichotomies and sacred trinities are broken down, replaced by eerily distorted triptychs throughout the novel. After being picked up by the Avondale, Jim becomes acquainted with the fate of the *Patna*, which does not in fact sink. Only then is Jim truly aware of the loss of his honor. Jim is strangely buried, paradoxically both dead and alive (or, better, undead).
Awaiting trial and relating his tale to Marlow, Jim is repeatedly described as buried or as a shade. Jim passes his days awaiting trial, “buried in a long chair…coming out of his place of sepulture only at meal-times or late at night, when he wandered on the quays all by himself” (51). After the old world has been destroyed, Jim is unsure of his place in the new one. Commenting on his situation, Jim says, “I was so lost, you know” (79). Jim is “detached from his surroundings, irresolute and silent, like a ghost without a home to haunt” (51). As Marlow listens to Jim, he feels himself “overcome by a profound and hopeless fatigue, as though his [Jim’s] voice had startled me [Marlow] out of a dream of wandering through empty spaces whose immensity had harassed my soul and exhausted my body” (81). Through Jim’s tale, Marlow will descend with Jim and identify with the younger man to the point of physical empathy, identification and obsession that borders on possession, and which possesses the reader, who follows Marlow as he follows Jim through the series of underworlds to come.
Jim’s Gethsemane: The Mythic Malabar House

In the midst of Jim’s official inquiry, Marlow invites Jim to dine with him at the Malabar House, and it is here that Jim confesses to Marlow and Marlow is compelled to listen, then to identify. Jim confides to Marlow that he finds the inquiry to be “hell” (48). I will elaborate in a more general way on the ritual of confession toward the end of this essay; here, however, I simply wish to discuss the dynamics of this particular confession. The reader, along with Marlow, hears Jim’s confession in the underworld that the Malabar House becomes. The atmosphere of the Malabar House echoes that of the *Patna*, evoking the sense of another nether region in which Jim is being buried alive. In the dining room of the Malabar House, Jim seems buried in a bizarre crowd that includes “two nomadic old maids, dressed up to kill, [who] worked acrimoniously through the fare, whispering to each other with faded lips, wooden-faced and bizarre, like two sumptuous scarecrows” (48). These two underworldly old maids recall, along with the girl whose laugh is “innocent and empty as her mind” (48), the knitting women Marlow encounters at the beginning of *Heart of Darkness*, who also represent a curtailed version of the three Fates. The Malabar House dining room is “more than half full of people with a-hundred-pounds-round-the-world tickets in their pockets” (47). These diners are tourists, travelers similar to the Pilgrims on the *Patna* (and yet also very different, inasmuch as their presence in the exotic locale is the result of modern “progress” rather than traditional faith), unaware of their stop in Jim’s private hell.

The light and dark imagery employed throughout the novel in establishing the mood of an underworld and in perpetuating mystery is also present in the description of the Malabar House:

On little octagon tables candles burned in glass globes; clumps of stiff-leaved plants separated sets of cosy wicker chairs; and between the pairs of columns, whose reddish shafts caught in a long row the sheen from the tall windows, the night, glittering and
sombre, seemed to hang like a splendid drapery. The riding lights of ships winked afar like setting stars, and the hills across the roadstead resembled rounded black masses of arrested thunder-clouds. (48)

The darkness and the lamp globes of the restaurant mirror the dark sea and stars visible through the tall windows and both the interior and exterior scenes evoke not only an underworld but also the darkness and stillness of the deck of the *Patna* on the night of the disaster. As Jim tells the story of that night the distinction between the scene of the *Patna* and that of the Malabar House dims. Describing Jim as he tells his tale of the *Patna*, Marlow notes: "He was very far away from me who watched him across three feet of space. With every instant he was penetrating deeper into the impossible world of Romantic achievements" (51).

The world of "Romantic achievements" is subterranean, requiring artistic descent. Jim recreates for Marlow the bulging plate and the flaking rust, the unconscious sleepers and his expectation "to see the iron open out as I stood there and the rush of water going over them as they lay...." (52). Jim tells his tale so vividly that he shudders "profoundly, as if a cold finger-tip had touched his heart" in remembrance (52). Listening to Jim, Marlow "can easily picture him...in the peopled gloom of the cavernous place, with the light of the bulk-lamp falling on a small portion of the bulkhead that had the weight of the ocean on the other side" (52). Jim recreates for Marlow the destruction of his world, in the process destroying Marlow’s comfortable world, and preparing the reader for the genesis and destruction of Jim’s new world order in Patusan.

In the Malabar House, Jim relates how “he had been tricked” and “taken unawares—and he whispered to himself a malediction upon the waters and the firmament, upon the ship, upon the men” (59). In the midst of his telling, Jim laughs bitterly at being called a coward by the first engineer. Jim’s bitter laughter falls “like a blight on all the merriment about donkeys, pyramids, bazaars, or what not” taking place at the Malabar House dining tables (61). The tense silence of the *Patna* quells the touristic chatter of the Malabar House: "Along the dim length of the gallery
the voices dropped, the pale faces turned our way with one accord, and the silence became so profound that the clear tinkle of a teaspoon falling on the tessellated floor of the verandah rang out like a tiny and silvery scream” (61-62). This stillness recalls that of the Patna. The pale faces of the crowd seem to gaze back at Jim from an underworld in which he is on trial. In this dead silence, Jim “flung his arm out at the night beyond the stone balustrade” as though it was the night beyond the deck of the Patna (65).

Marlow and the reader are both caught up in Jim’s tale and in what Guerard refers to as sympathetic identification with Jim. At one point during his confession, Jim asks his confessor Marlow what he would do if he felt the house moving below him. Jim does not wait for the older man to answer; Jim answers, “Leap! By heavens! You would take one spring from where you sit and land in that clump of bushes yonder” (65). As the distinction between the scene of the Malabar House and that of the Patna is obscured, so is the distinction between Jim and Marlow. Disturbed, Marlow doesn’t answer, but does, “with a rapid glance, estimate the distance to the mass of denser blackness in the middle of the grass-plot before the verandah” (65-66). Time and location become confused as Marlow recognizes himself in Jim.

Time, symbolically, is disrupted in the Malabar House as it is on the Patna and in the lifeboat. Jim’s wish to die in the lifeboat merges with his wish to die in the restaurant: “I wish I could die” (68), he tells Marlow. To demonstrate his stance on the lifeboat as he contemplated suicide, Jim “perched himself smartly on the edge of the table and crossed his arms....” (72). For Jim, telling and reenacting combine to reinforce the hellish indistinguishability of the Malabar House table and the Patna lifeboat. Jim seems to be in both underworldly places and yet in neither: “His hand groped stealthily, came in contact with a liqueur-glass, and was withdrawn suddenly as if it had touched a red-hot coal” (71).

At work in the Malabar House interview are both the dynamics of confession and the compulsion of identification. Marlow encourages Jim to finish his tale because he needs to hear it: “I pushed the bottle slightly. ‘Won’t you have some more?’ I asked” (71). As Jim relives the
anger he felt when he realized he had jumped ship, his anger resurges: “He looked at me angrily. ‘Don’t you think I can tell you what there is to tell without screwing myself up?’ he asked” (71).

As the evening and the tale unwind, Jim and Marlow are alone with each other in Hades with Jim’s Eastern bride looking on: “The squad of globe-trotters had gone to bed. We were alone but for a vague white form erect in the shadow....” (71). This vague white form, Jim’s Eastern bride, follows him to Patusan. Briefly glimpsed here, in the midst of the relation of the Patna incident, she only reinforces Jim’s failure to realize the opportunity to act heroically, and Marlow’s acknowledgement of her ghostly presence indicates his descent into Hades with Jim and his new capacity for seeing what Jim sees.

Not only does the Malabar House merge with the Patna, but the scene gets progressively hellish, and Jim explodes in a climax where the narrating and narrated worlds are violently conflated. Jim, caught up in describing the struggle with the crew on the lifeboat, “with a convulsive jerk of his elbow knocked over the cognac bottle” (73). The shattering cognac bottle only reinforces the tensions of Jim’s sense of the conflict on the Patna. At the sound, “He bounced off the table as if a mine had been exploded behind his back, and half turned before he alighted, crouching on his feet to show me a startled pair of eyes and a face white about the nostrils” (73). Jim is in his most defensive stance when the Malabar House is at its darkest moment. “The lights,” Marlow notes at this point, “had been put out in the dining hall; our candle glimmered solitary in the long gallery, and the columns had turned black from pediment to capital” (73). The floor of the Malabar House here, phantasm-like, transforms into the deck of the Patna. Marlow’s description of Jim implies that Jim is wherever he imagines himself to be: “He passed on a few steps to the imaginary end of his beat, and when he flung round to come back both his hands were thrust deep into his pockets” (78).

Marlow’s vision of Jim in the Malabar House not only takes us back to the Patna but foreshadows his vision of Jim on the coast of Patusan:
The dim candle spluttered within the ball of glass, and that was all I had to see him by; at his back was the dark night with the clear stars, whose distant glitter disposed in retreating planes lured the eye into the depths of a greater darkness; and yet a mysterious light seemed to show me his boyish head. (78)

The light illuminating the boyish head recalls the halo of Christ in Christian iconography and Jim’s emotional hell recalls Gethsemane, though Jim’s visit to Marlow’s room is actually more similar to Christ’s cathartic experience in Gethsemane than is his confession in the dining-room. The white form of Jim’s Eastern bride is reminiscent of the bride of Christ and the ghostly bride of Orpheus. The combination of all the white and dark imagery recalls Allon White’s discussion of Conrad’s use of such imagery in his rhetoric of enigma. The darkness behind Jim recedes into, and directs the reader’s attention toward, greater darkness. Of the light and the darkness, it is actually the light around Jim’s head which Conrad refers to as “mysterious”; the light of the clear stars lures the eye into the deeper mysteries behind Jim’s boyish face.

While Jim continues to pace, the atmosphere of the Malabar House continues to recall that of the Patna, the stillness of the lifeboat, and the grave: “All around everything was still as far as the ear could reach” (81). In this stillness in the Malabar House, Marlow notices:

The mist of his feelings shifted between us, as if disturbed by his struggles, and in the rifts of the immaterial veil he would appear to my staring eyes distinct of form and pregnant with vague appeal like a symbolic figure in a picture. The chill air of the night seemed to lie on my limbs as heavy as a slab of marble. (81)

Marlow may frame Jim as “a symbolic figure in a picture,” but this ability to look at Jim in a painterly fashion, as a distanced observer, is nonetheless matched by a sympathetic identification with Jim so complete that he feels a corpse himself. This is the fateful identification described by Ian Watt, the mirror-process mentioned by White, and what Blanchot refers to as meeting the gaze of the other. As Jim describes the coldness of the lifeboat, Marlow feels the chill of the grave, and he too seems buried alive. While Jim concludes, “Dead or not dead, I could not get
clear” (82), the reader discerns that Marlow cannot get clear either. Throughout the novel, Jim is neither dead nor alive: he is one of the undead, going from one underworldly environment to another in a series of initiations that ultimately fail to initiate anything or anyone besides Marlow and the reader. The stillness for Marlow sounds the end of his faith in the traditional code of honor, the “pre-creation slumber” (Guth) preceding an awakening into a new world in which Marlow will no longer be just himself but also Jim.

This awakening initiates Marlow’s inquiry into his own system of beliefs—an inquiry that parallels the official inquiry into Jim’s conduct aboard the *Patna*. The underworldly scene of the Malabar House gives way to that of the inquiry, which attempts to cast the light of the law upon Jim’s dark actions, but cannot. Marlow himself remarks that the object of the official inquiry itself “was not the fundamental why, but the superficial how, of this affair” (35). He complains, “You can’t expect the constituted authorities to inquire into the state of a man’s soul” (35), which is what Marlow is, in fact, interested in. Marlow’s interest is “purely psychological—the expectation of some essential disclosure as to the strength, the power, the horror of human emotions” (35). When Marlow shakes Jim’s hand at the close of the inquiry, he acknowledges his connection to Jim. They shake and “the candle spluttered out, and the thing was over at last, with a groan that floated up to me in the dark. He got himself away somehow. The night swallowed his form” (95). From Marlow’s point of view, Jim is always descending or disappearing. Marlow cannot see Jim but can “hear the crunch-crunch of the gravel under his boots. He was running. Absolutely running, with nowhere to go to. And he was not yet four-and-twenty” (95). Marlow emphasizes Jim’s youth because Jim represents Marlow’s youth. If Marlow cannot create meaning for Jim, he cannot generate it for himself either.

Marlow describes his communion with Jim in the Malabar House in terms reminiscent of the Last Supper: “Our communion in the night was uncommonly like a last vigil with a condemned man” (92). Already, Marlow is rendering Jim in Christ-like terms. After the trial, Jim experiences the equivalent of Christ’s vigilant prayers in Gethsemane in Marlow’s room. Having served as
confessor in the Malabar House, Marlow serves as the Father who hears Jim’s prayers and decides Jim’s fate. In Marlow’s room, Jim does “have it out with himself without being bothered by the rest of the universe” (104). Jim struggles with his inner demons, “alone with his loneliness” (104), while Marlow pointedly ignores him and writes letters which will direct the passive Jim’s fate. Marlow’s purposeful and effective writing reiterates his role as artist, shaping Jim’s life as he considers then rejects the idea of referring Jim to Chester. While Marlow takes “refuge in the letters” (105) against the violence of Jim’s emotions, Jim is wracked by an emotional storm. Jim “was rooted to the spot, but convulsive shudders ran down his back; his shoulders would heave suddenly” (105). Marlow is a witness, a confessor, and a recorder of Jim’s personal hell.

The scene in Marlow’s room becomes darker and hellish like the Patna, the lifeboat, and the Malabar House as dusk falls; Marlow writes by candlelight, and Jim faces the darkness of the night alone. Jim’s emotional storm drives him out onto Marlow’s verandah: “he rushed out on the verandah as if to fling himself over—and didn’t” (108). Marlow’s verandah and the expression of the suicidal impulse recall the Malabar House verandah and the deck of the Patna. Just as on the deck of the Patna, a literal storm coincides with Jim’s emotional storm. As Jim struggles emotionally, Marlow also experiences “that profound disturbance and confusion of thought which is caused by a violent and menacing uproar—of a heavy gale at sea, for instance” (105). Marlow’s anxiety and storm metaphor indicate his intensified identification with Jim, while his description of Jim in terms of light and dark imagery continues his earlier rhetoric of enigma. Marlow views Jim’s silhouette by candlelight: “he stood on the brink of a vast obscurity, like a lonely figure by the shore of a sombre and hopeless ocean” (105). Jim is “distinct and black, planted solidly upon the shore of a sea of light” (108). This switch from sombre ocean to sea of light seems to anticipate Jim’s future heroic success in the midst of this dark tribulation, but Jim’s tribulation here overshadows his later success: “I shall always remember him as seen through the
open door of my room, taking, perhaps, too much to heart the mere consequences of his failure” (107), mourning the death of a Romantic dream that has no place in a modern world.

Jim, “so grave and youthful” (111), so Romantic, appeals to modern Marlow as a fragment of a lost self. Jim’s fine sensibilities provoke Marlow’s decision: “But he was too interesting or too unfortunate to be thrown to the dogs, or even to Chester” (108). In writing Jim a recommendation that allows him to start over as a water clerk, Marlow expresses faith in Jim that gives the younger man confidence and a renewed resolution to realize his Romantic dreams in a new direction—East and towards Stein, through yet another underworld. While Jim leads Marlow into the underworlds of the *Patna* and transforms the Malabar House dining and hotel room into underworlds, it is Marlow who leads Jim and the reader to Stein and to Patusan. Before bringing Jim, Marlow first visits Stein’s Hades-like home himself.
(vii) **Stein’s Underworld**

The *Patna* incident becomes part of maritime folklore, a legendary underworld episode from which Jim cannot escape. While one character sagaciously comments that nearly everyone has jumped off of one *Patna* or another, Marlow never admits to failing either himself or the seaman’s code, even as he jumps ship vicariously with Jim in the underworldly Malabar House dining room. Years later, when Marlow realizes that his new start for Jim will not do, that the *Patna* episode will not sink, he voyages to Stein’s underworldly home for a consultation. Marlow enters Stein’s home late in the evening: like the *Patna*, the Malabar House restaurant, and Marlow’s room, it is a dark and silent place, described in terms of light and dark imagery that evokes the realm of the dead. Stein’s Javanese servant leads Marlow through a dimly lit dining-room to the door of Stein’s study; the servant vanishes after announcing Marlow, “as though he had been a ghost only momentarily embodied for that particular service” (123-124). Stein’s home is a house of shades.

In this sacred underworld, Stein's writing desk and his insect specimens stand out from the darkness, connecting his artistry and death. Stein’s study is a dark “spacious apartment” with a strongly lighted writing desk in one corner; it gives an overall impression of “shapeless gloom like a cavern” (124). The underworldly atmosphere of the study is increased by the “narrow shelves filled with dark boxes of uniform shape and colour [that] ran round the walls, not from floor to ceiling, but in a sombre belt about four feet broad” (124). These lined-up coffins form “catacombs of beetles” (124), which reinforce the sense that Stein is a ruler of the land of the dead. In his old age, Stein “lived solitary…with his books and his collection, classing and arranging specimens” (126). Among the last specimens he classes and arranges will be Jim and Jewel.
When Stein talks to Marlow of his dead wife and child in Patusan, he strikes “a match, which flared violently” (126). This match recalls those struck by Marlow himself as he interrupts the frame of his tale from time to time to comment to his audience of listeners. This flare of light in the darkness also recalls the light and dark imagery that links each Hades-like setting and emphasizes Jim’s enigmatic nature. In this dark room, Marlow describes Stein as “the shadow prowling amongst the graves of butterflies” (130), moving in and out of the ring of light created by the writing lamp. Marlow asks Stein for guidance in Jim’s case. Stein “lit a two-branched candlestick and led the way…. through empty, dark rooms” (131). Marlow follows the “gleams from the lights Stein carried” (131), unable to discern the older man—who tends to disappear like Jim—in the darkness, following him through a void like that of Jim’s lifeboat:

They [the lights] glided along the waxed floors, sweeping here and there over the polished surface of a table, leaped upon a fragmentary curve of a piece of furniture, or flashed perpendicularly in and out of distant mirrors, while the forms of two men and the flicker of two flames could be seen for a moment stealing silently across the depths of a crystalline void. (131-132)

Stein’s two flames recall the lights of the Patna, the stars outside the windows of the Malabar House, the candlelight of Marlow’s room and every match struck in the midst of a narrative in the novel. These lights draw the reader’s attention back to the narrative frame as part of Conrad’s efforts to reinforce the importance of tale-telling and the teller’s efforts in overcoming the “crystalline void” of modern alienation.

Marlow follows Stein as blindly as Jim follows Marlow back to the latter’s room for guidance. As they progress through the darkness, Stein diagnoses Jim as a Romantic. Stein, like Jim in the Malabar House, has the darkness at his back, and Marlow realizes that Stein, himself a Romantic, is for that reason the best authority on Jim’s fate. “With his head dropping on his breast and the light held high he began to walk again” (132): Stein’s stance here foreshadows Doramin’s and the French Lieutenant’s and reinforces the truth he reveals, albeit as yet another fragment, to Marlow.
Marlow sees this truth in an epiphanic moment as Stein leads him through a descent into “pellucid depths” to a truth that Marlow cannot grasp on his own:

I saw it vividly, as though in our progress through the lofty, silent rooms amongst fleeting gleams of light and the sudden revelations of human figures stealing with flickering flames within unfathomable and pellucid depths, we had approached nearer to absolute Truth, which, like Beauty itself, floats elusive, obscure, half submerged, in the silent, still waters of mystery. (132).

Conrad’s rhetoric again confirms the enigma; Marlow descends to Truth which is “obscure” and “half submerged, in the silent, still waters of mystery.” In the course of this descent, Marlow cannot see Stein, only the gleaming lights that indicate his movements: “He preceded me. My eyes followed his movements...” (132). Stein is an absence, a mystery leading Marlow to greater mystery. This descent, Stein’s appeal, and the truth to which he leads Marlow, are analogous to the artistic descent described in Conrad’s Preface to The Nigger of the Narcissus. The thematic purpose of Stein’s underworldly home is to situate Stein in that subterranean world into which a Conradian artist must descend, in accordance with Conrad’s artistic manifesto in the Preface. From this Hades, Stein charts the course of Marlow, Jim, and the reader for yet another uncharitably mysterious underworld, the land of impossible dreams, Patusan.
Jim’s descents and his quest begin on the pilgrim ship, where he dreams his dreams, and end in Patusan, where he lives his impossible dream; Marlow’s vicarious descent and personal quest begin with Jim’s tale of the Patna, take him to Patusan, and end with the reader. Critics frequently cite the apparent division of Lord Jim into two completely different novels—the Patna episode and the Patusan episode—as a structural weakness. Semantically, however, the name of the ageless ship and the name of the ageless country recall each other; thematically, both the Patna and Patusan function as feminized underworlds, zones of the subconscious, realms of artistic descent. Just as the scene shifts in the second half of the novel, so do Conrad’s narrative modalities. The disrupted chronologies, thematic appositions, and overlapping inquiries of the first half of Lord Jim (all identified by Ian Watt as central to Conrad’s impressionism and the process of prolonged psychological probing it makes possible) give way to the more straightforwardly simple narration of the Patusan section as a result of what Watt refers to as Conrad’s “progression d’effet.”

Conrad described in a letter to Garnett his use of light and dark imagery to achieve metaphorical spotlighting, and Watt has commented that, “After the brilliant spotlights playing starkly on every detail of human inadequacy and weakness in the first part, the lighting changes” (Watt, 309). Jim’s inadequacy is starkly explored in the Patna section of the novel; by contrast, both Jim and Patusan initially appear in a softer light. Watt notes the narrative disparity in Patusan as a structural flaw but inadvertently reveals the change in narrative technique to be necessary when he states that Patusan has to remain slightly out of focus to achieve the effect of the dream brought to life. Conrad changes to a more lurid lighting again at the novel’s end as Jim
and his dream dies: “for the catastrophe there is a sudden wrenching change to a spotlight of a
more livid hue, which illuminates the dying Jim in the stark contours of melodrama” (Watt, 309).

Patusan has to remain out of focus because it is the world of impossible dreams, the domain of
the unconscious, the underworld of Jim’s final descent. In terms of the rhetoric of enigma, Jim is
now described as white against a dark background, but both Jim and Patusan are obscured.
Neither can appear too clearly or the mystery will be shattered. Watt explains Patusan as an
“‘other’ world” (Watt, 308) in which the psychological probing found in the first half of the novel
is impossible because of the Romantic nature of the setting and plot. In Patusan, Conrad is no
longer “dealing with realities that can stand up to three-dimensional scrutiny” (Watt, 308). Events
such as “Jim’s triumph over Sherif Ali … would be revealed for the Romantic schoolboy
adventures that they essentially are if they were subjected to the extended and rigorous cross-
examination which is applied to Jim’s desertion of the Patna” (Watt, 308). Patusan is feminized,
Romantic, primordial, a subconscious dream world, the-destructive element in which Jim is
immersed.

Patusan is feminized by its association with Jewel and by the blatantly feminine contours of
the land. Andreach finds in the split-hills imagery of Chaper 21 an image of descent and birth
subtly sexual and indicative of how Patusan’s landscape “imagistically defines the process of
redemption” (Andreach, 59). Forty miles upriver from the sea, when the first few houses appear
in Patusan, so too do “the summits of two steep hills very close together, and separated by what
looks like a deep fissure, the cleavage of some mighty stroke” (134). At this same location,
Marlow watches the moon ascend “ruddily…gliding upwards between the sides of the chasm, till
it floated away above the summits, as if escaping from a yawning grave in gentle triumph” (135).
This image transforms the landscape of Patusan into a strange world “foreign to one’s memory”
(135), and also reinforces the function of Patusan as a grave for Jim and as a source of renewal
for Marlow. Orphic Marlow alone escapes the yawning grave of Patusan.
When Brierly, Marlow, and Stein talk of burying Jim during and after the inquiry, their talk reinforces Jim’s descending identity and suggests his mythical function as a vegetative god. Chester’s suggestion of Walpole Island as a fertile and practical grave for Jim, where Jim would in effect become a slave driver exploiting the dark-skinned manure shovellers, offsets the more fertile landscape of Patusan in which Jim exploits the dark-skinned natives to their (supposedly) mutual benefit. After the inquiry, Marlow compares Jim’s wounded spirit to “a bird with a broken wing...[that might] flutter into some hole to die quietly of inanition” (112). Jim’s wounded spirit is reborn in Patusan in Christ-like terms; dressed in white, he first brings peace and hope, and later dies with outstretched arms in atonement for his own sin.

Stein implies Patusan’s function as the destructive element when he first diagnoses Jim’s need to immerse himself in the destructive element, then Marlow sends Jim there to get him out of the way of himself and everyone else. Stein says that in order to find redemption, Jim should, “In the destructive element immerse!...To follow the dream—and again to follow the dream—and so” (131). Following a dream figuratively entails artistic descent. Following a dream literally entails a descent into the subconscious, with its associations with sleep, dreams, and death. Marlow—sure that sending Jim to Patusan is the equivalent of sending Jim to his death or to “a star of the fifth magnitude” (133) from which he will never return—gives Jim a revolver to take with him, and then desperately rushes the forgotten cartridges to him. More people actually die in Patusan than in any other setting in the novel.

More descents are also enacted in the Patusan section than in the other underworlds of Lord Jim. Jim figuratively descends into the underworld of Patusan, even though, ironically, he must ascend a river to do so. Soon after, Jim makes two leaps to escape the Rajah’s stockade that lead to his vivid rebirth as he struggles from the muddy riverbank in the underworldly womb/tomb of Patusan. When Jim kills one would-be assassin and forces the remaining assassins to jump in the river, he recreates through others his leap from the Patna just as surely as he does earlier at an Eastern port when he tosses a fellow employee into the harbor.
Even when expressing surprise at the glory to which Jim rises in Patusan, Marlow affirms that no one could possibly know of Jim’s Romantic achievements in Patusan through any medium other than himself. As the primary artist in *Lord Jim*, Marlow has unique access to this Romantic, primordial, or subconscious world of impossible dreams. The only person who knows more of Patusan than Marlow or Jim is the fading master artist, Stein. Patusan becomes associated with artistry when Marlow describes it as a work of art, “a picture created by fancy on a canvas, upon which, after long contemplation [like Eurydice, or the unknown], you turn your back for the last time” (200). Marlow’s reference to Patusan as a picture, a framed reality, recalls his earlier comparison of Jim to a symbolic figure in a picture pregnant with appeal. In Patusan, the mythic imagery surrounding Jim proliferates and his symbolic nature culminates. Jim and Jewel are both trapped in the picture/grave/Hades of Patusan. Jim dies there, and Jewel is one “of the living who, buried in remote places out of the knowledge of mankind, still...[is] fated to share in its tragic or grotesque miseries” (196). Though she ends up in Stein’s home, Jewel no more escapes the underworld of Patusan than does Jim.

Conrad creates in Patusan a Romantic world of impossible achievements and truths, and Marlow recreates it for his audience. As such a creation, Patusan is the place not for reason but for intuition (which, again, establishes another stereotypical association with the feminine). Jim’s intuition guides him to rebirth and then final death in Patusan. Marlow, too, experiences rebirth when visiting Patusan. It is to the illusionary underworld of Patusan that Marlow descends for final truths concerning self, heroism, artistry, and existence. If “the journey to self-discovery is an interior journey into death and life on a feminine landscape” (Andreach, 43), then Patusan is the feminine landscape in which Jim both discovers and destroys himself, and in which Marlow and the reader discover themselves. Andreach argues that Patusan’s “blatantly feminine contours imagistically define the process of redemption as a journey to the limits of life and a rebirth through the agency of the heroine” (Andreach, 59). The heroine in *Lord Jim* is as much Patusan as it is Jewel.
Marlow recalls Patusan and the fragments of truth he discerns there but he will cathartically—through telling his tale—escape this world of impossible dreams:

I had looked under its obscure surface; and I felt that when to-morrow I had left it for ever, it would slip out of existence, to live only in my memory till I myself passed into oblivion. I have that feeling about me now; perhaps it is that feeling which has incited me to tell you the story, to try to hand over to you, as it were, its very existence, its reality—the truth disclosed in a moment of illusion. (196)

This description of Patusan’s tenuous reality recalls Marlow’s statements concerning himself as the sole mediator of Jim’s reality to the rest of the world. His reference to Patusan’s obscure surface recalls Jim’s veil of inscrutability, and is part of the rhetoric of enigma that structures so much of Conrad’s narrative—a rhetoric that relies upon the twin ideas of a mysterious truth being disclosed in a moment of illusion and of an artist who can provide the illusion that will make this truth discernible to his audience.

Marlow evokes Patusan’s primordial, or a-historic, nature, calling it “one of the lost, forgotten, unknown places of the earth” (196). This exotic stereotype of a primordial world—which still finds its way into some contemporary criticism, as when Guth speaks of Heart of Darkness’s Africa as “the world before the advent of time” (Guth, 159)—is obviously important to Lord Jim’s Patusan. Indeed, I would argue that Marlow, and Conrad’s, evocation of this primordial nature is more than a reductive colonial stereotype. Patusan must seem like a land in an earlier stage of development because the Romantic must precede the modern, and because Patusan is steeped in the same timelessness as the Patna. Jim does go back in time, in a sense, when he recovers his lost worth in Patusan. His inability to mend the broken clock in the Rajah’s stockade indicates Patusan’s timeless nature and recalls the suspension of time aboard the Patna. In Patusan, Jim finds what, according to Guth, Kurtz finds in Africa: “a far more threatening image of elemental being, of wild and as yet unharnessed natural forces” (Guth, 159). Jim briefly
harnesses the natural forces of his imagination, of fear and of “primitive” man’s sense of wonder, to create his own doomed Eden or Camelot in which he is Lord.

Patusan is a return to a more idealized past and a more idealized sense of man's capacity. Gail Fraser notes that “in the Patusan section of Lord Jim Conrad uses symbolic images and mythic allusions to emphasize the growth of Jim’s moral sense and, consequently, the relationship between moral identity and ‘exalted’ egoism” (Fraser, 96). Jim becomes, in Patusan, the more godlike Lord Jim. Mythic allusions to Christ and to Camelot emphasize how Jim’s selfish egoism serves the seemingly selfless moral purpose of providing order, peace, and security for the natives: “Marlow’s comparisons of Jim with a knight in a medieval legend (312) and a hero of Greek mythology (267) suggest that man is capable of becoming more godlike than he really is” (Fraser, 103). Linking Patusan with Romantic realms such as Camelot invokes man’s idealistic vision and sense of wonder and the impossibility of realizing such noble aspirations for more than a short time. Patusan is the universal realm of Romantic wonder into which Jim penetrates: “With every step he was penetrating deeper into the impossible world of Romantic achievements” (51).

Jim’s Camelot kingdom in Patusan replicates Stein’s original enterprise and alliance with Doramin. Given the foggy history of Stein’s earlier imperial exploitation of Patusan and the interminable rivalry of various tribal factions, including those of the Rajah and Doramin, Jim’s emulation of Stein in Patusan is another form of return to the past. Viewed in historical terms, of course, the irony is that this discovery (and recovery) of Romantic wonder is inseparable both from colonial intrusion and from Jim’s attempt to enforce the nineteenth-century moral code that he had failed to uphold when he leaped from the Patna. Jim’s wonder ceases with him; more wonder-full is the thought-provoking and enigmatic tale Marlow tells of Jim's self-entombment in Patusan.

Like Kurtz, an imprisoned self-appointed god, Jim is a self-appointed Lord who cannot leave. When Guth calls Kurtz a figure in whom “the mythic past and the retributive present” meet (Guth, 161), she inadvertently describes Jim as well. Jim is Adam and Eve seduced by Gentleman
Brown and destroying paradise, causing "the death-throes of a primordial world" (Guth, 161), and marking the beginning of time in a fallen or modern world. Patusan is elemental, or primordial, not only in stereotypical, colonial terms, but in the metaphoric terms of artistic descent. Patusan is the destructive element in which Jim immerses himself on his quest for redemption. Andreach compares Jim to Kurtz, asserting that in making the mythic descent into himself that every man must make, Jim does not affirm his link to man but goes farther into the unknown than common man in order to break this link. Like Kurtz, Jim becomes:

a captive of the interior he set out to conquer. The confluence of his illusion and that of the Patusan natives allowed him to become 'wholly other.' He did climb out of the mud bank into which he leaped shortly after his arrival, "'cracking the earth asunder'" (XXI. 254), but at a terrible price: he forfeited his membership in a human community. (Andreach, 58)

Jim may forfeit his membership in a human community, as Andreach argues, but he remains inextricably deposited in the human subconscious, and as such his links with the world are not in the final analysis severed. Indeed, Jim's story—and the end of that story—may threaten Marlow's faith in original and attainable perfection, but not in solidarity. While various aspects of the novel are ambiguous, for Conrad, the artist is the hero, descent is necessary for creation and regeneration, and they both make possible the solidarity that emerges in Lord Jim as the only answer to modern isolation. The artist is the hero capable of communicating man's solidarity in the face of the unspeakable through the weaving of his tale.
Andreach’s condemnation of Jim takes into consideration neither the conflict of the Romantic and the modern nor the importance of the heroic code of conduct in *Lord Jim*. Jim chooses the one form of self-realization that Jewel cannot initiate, the salvation of his honor and the retention of his nobility. This honor and nobility is part of the Romantic code of conduct Jim betrays in abandoning the *Patna*. Jim’s suicide salvages, for him, his link with the world through adherence to this heroic code that was severed when he leapt from the *Patna*. If Jim’s ritualistic suicide is interpreted as a rejection of his humanity as argued by Andreach, then the code of conduct governing men’s lives in *Lord Jim* is negative and arbitrary, and Jim’s suicide can be nothing more than an empty gesture in support of an equally empty code. Marlow questions but never rejects this code, just as he questions Jim’s suicide but never condemns it either. Alive with Jewel or dead in Patusan, Jim’s link with society is severed the moment he jumps from the *Patna*—until his confession to Marlow inextricably links them forever, and perhaps salvages the essence of the unsalvageable code to which both men questioningly subscribe.

When Marlow refers to Jim as “one of us,” it may be the case that he is referring to himself as isolated from the rest of humanity along with Jim. This recurring phrase actually refers to God’s description of Adam and Eve after the Fall as belonging to the community of God and the angels that knows the difference between good and evil; this allusion to Genesis 3:22 groups Marlow, Jim and the reader as among the fallen. Marlow seems to operate from within the code of conduct governing his society, but he nonetheless calls this code into question. Andreach’s interpretation of the hero’s quest in *Lord Jim* does not address in depth the code of conduct which Marlow *seems to* and which Bob Stanton, Brierly, and the French Lieutenant Bob Stanton *do*
endorse. Before continuing on with an account of the remainder of the novel (notably, the appearance of Gentleman Brown and his role in the final fall, or leap, of Jim), I would like to discuss here this code of conduct as it relates to the heroism of Stanton, Brierly, and the Frenchman. These heroic doubles live and die according to the seaman’s code of conduct—in Brierly’s case, he dies in order to avoid breaking it. All three of these heroes also enhance the mythic substructure of the novel by doubling Jim, Marlow or Stein, and their functions as doubles are relevant to an understanding of the end of the novel, and to Conrad’s intentions as a whole.

Jim betrays the seamen’s code of heroic conduct when he jumps from the Patna; ironically, in Patusan, Jim dies trying to recreate this same honorable code of conduct. To Marlow, educated by Jim’s successes and failures on the Patna and in Patusan, “the codes binding individual to community appear illusory if not capricious. The social world’s ability to fend off external chaos through habit and duty is thus imperiled” (Lynn, 35). The arbitrariness of these communal codes points toward the relativism of modernity. David Lynn suggests that it is ultimately through Marlow that meaning, if not the code, can be redeemed. Marlow is the dynamic hero who “awakens to social truths he has never before dared question” (Lynn, 31) as a result of his encounter with the series of underworlds into which he descends with Jim. For Marlow, “the ‘fixed pattern of conduct’ is no longer adequate; it is replaced with the ironic juxtaposition of such fundamental human values as solidarity, labour, and love, against a radical skepticism” (Lynn, 42). Lynn explains that Marlow’s task in staying true to Jim and in telling the tale is “no less than to reweave the moral fabric of human endeavor” (Lynn, 35). Telling his tale—acknowledging the threatening darkness and recognizing the importance of solidarity, labor and love in combating it—is Marlow’s duty and his Orphic heroism (as previously affirmed by Strauss).

Andreach may posit Marlow as the true Conradian hero of Lord Jim, but Jim is also a hero, though his heroism is the most questioned. Andreach takes a strong stand in condemning Jim’s chosen method of redemption at the end of the novel; however, Conrad is rather more nuanced in
his attitude toward Jim than Andreach will allow for. Andreach’s exploration of slain and 
resurrected gods does not differentiate between modern and Romantic heroes. Jim is a Romantic 
hero and Marlow’s tale is an elegy honoring this problematic Romantic hero. Jim’s ritualistic 
death is his final descent and union with his chosen Eastern bride. Marlow’s response to Jim’s 
abandonment of Jewel is ambiguous. Rather than criticizing Jim’s decision, Marlow defends 
Jim’s honesty. Marlow’s identification with Jim renders them doubles of one another. But, as 
Andreach points out, “That everyone is a double for everyone else is implicit throughout 
Conrad’s writings, since everyone shares the actual and potential reality of the human condition” 
(Andreach, 96).

Duty and heroism connect each of the doubles who form the dynamic framework for Jim’s 
heroism. Jim is doubled or foiled not just by Marlow but by a series of heroes or anti-heroes 
throughout Lord Jim. Each of these heroes or anti-heroes either accepts or rejects the code of 
conduct, or inadvertently reveals its absurdity. Each double is engaged by duty or heroism or 
artistry. While Jim abandons ship and Marlow and Jim both abandon Jewel, Little Bob Stanton 
refuses to abandon woman or ship in a comic suicide that recalls the suicides of Brierly and of 
Jim but that seems absurd in comparison with those ostensibly heroic examples, in turn making 
the code of conduct that kills Stanton seem absurd.

Marlow interrupts his narrative confession to the French Lieutenant to tell the apparently 
marginal story of Stanton, so that Conrad can remind the reader exactly how Jim falls short and 
provide another recurring image of descent in the novel. Little Bob Stanton follows the code of 
conduct to the letter, both doubling and foiling Jim. Stanton is unquestionably what a hero should 
be, though his comic physical description and destruction offset the Romantic glamor of Jim’s 
lordly appearance and heroic crisis. Stanton dies in an act of practical heroism—he goes down 
with woman and ship while trying to save an hysterical lady’s-maid from the sinking Sephora. 
Jim dies in an act of Romantic heroism, a suicide act that preserves his Romantic image of 
himself and his honor but serves no practical purpose. Stanton, like Jim, suffers the “mode of life
more barren of consolation, less capable of being invested with a spark of glamour—unless it be the business of an insurance canvasser” (91). Stanton’s experience, however, is the reverse of Jim’s. Stanton is first exiled from the sea because “of the complications of a love affair” (92), and then returns to the sea to encounter a fateful collision.

Stanton’s fateful descent is very disparate from Jim’s because Stanton is a foil to the real Romantic hero, Jim. Unlike the abandoned pilgrims of the *Patna*, all of the *Sephora*’s passengers have been cleared off the ship save the crazed lady’s-maid, who “held to the rail like grim death” (Conrad, 91). Rather than a Romantic rescue, Stanton’s gallant efforts result in a comic “wrestling match” (91) between “the shortest chief mate in the merchant service,” (91) and the maid, who “stood five ten in her shoes and was strong as a horse” (91). A deck hand, “hiding a smile at the recollection” (91), tells Marlow, “‘It was for all the world, sir, like a naughty youngster fighting with his mother’” (91). Practical Stanton stops struggling with the girl hoping to save her when the watery rush might tear her from the rail (91-92). Unfortunately, Stanton’s pragmatism, duty, and patience cost him his life. The ship sinks and the survivors “never saw anything alive or dead come up” (92). Like Jim’s, the story of Stanton’s collision is passed on by word of mouth—but as a comic story rather than as a tragic twist of fate and dishonor.

Despite the grim description of the suction of the sinking ship, rather than contemplating Stanton’s death as a tragic loss, Marlow recollects it with amusement, perhaps because Stanton’s gnome-like stature is so unheroic. In contrast to Jim’s tall, blond, blue-eyed, handsome figure dressed impeccably in white, Marlow recalls Stanton as “undersized and bearded to the waist like a gnome” (92). Whereas Stanton’s love life, work as a water-clerk, and death served to amuse Marlow, Jim’s love affair with Jewel, work as a water-clerk, and death saddens and confuses Marlow—revealing, to say the least, a possible double standard at the heart of the manly code to which he subscribes. Immediately after completing the anecdote about Stanton, Marlow incorporates Stanton’s comment that because of the shore work, his “immortal soul shrivelled down to the size of a parched pea after a week” (92). In this manly world, as it were, size matters.
Marlow then returns to the serious topic of Jim's sensitive and suffering soul, the "punishment for the heroics of his fancy—an expiation for his craving after more glamour than he could carry" (92), his larger-than-life stature notwithstanding.

Because Stanton's final actions are a heroic though comic suicide, Stanton foils and doubles Jim in Conrad's process of manipulating the reader's response to Jim. Stanton, the descending gnome, and the "priest"-like (85) French Lieutenant are two true heroes according to the standard of conduct or maritime code of Lord Jim. Marlow's failure to praise Stanton's heroism and emphasis on the buffoonery of his heroic endeavor should cause the reader to question Marlow's authority on heroism and Marlow's judgment about Jim. The condemnation of Jim by the French Lieutenant, who understands that "'Man is born a coward'" (90), but who does not, as Marlow first assumes, take "a lenient view" (90) of Jim, also calls into question Marlow's bias in favor of Jim. The French Lieutenant condemns Jim in terms that foreshadow Doramin's final and fatal condemnation of Jim at the novel's end:

He drew up his heavy eyelids.... I was confronted by two narrow grey circlets, like two tiny steel rings around the profound blackness of the pupils. The sharp glance coming from that massive body, gave a notion of extreme efficiency, like a razor-edge on a battle-axe. (90)

Doramin is similarly elderly and massive and the double-barrel gaze of the French Lieutenant, made up of "two narrow grey circlets," mirrors the pistol barrels that Doramin will later efficiently level at Jim's chest.

The lieutenant's final words concern the loss of honor:

I contended that one may get on knowing very well that one's courage does not come of itself.... There's nothing much in that to get upset about. One truth the more ought not to make life impossible.... 'But the honour—the honour, monsieur!... The honour... that is real—that is! And what life may be worth when....the honour is gone...—I can offer no opinion. I can offer no opinion—because—monsieur—I know nothing of it.' (90)
The French Lieutenant, like Bob Stanton, knows nothing about life without honor, because he has adhered to the code of honor that applies to all seamen. Had the wounded Patna sunk, the dutiful lieutenant, like Stanton, would have gone down with the ship in the course of his duty. Does this performance of duty make him a hero? Or simply a performer? Neither the lieutenant nor Stanton abandon ship and passengers as Jim does, though both face life-threatening danger. Both the Frenchman and Stanton are “steady reliable men who are the raw material of great reputations... uncounted lives that are buried without drums and trumpets under the foundations of monumental successes” (87), but Marlow only recognizes this reliability and steadfast heroism in the Frenchman. The French Lieutenant adheres to duty when he stays aboard the wounded Patna for thirty heroic hours. Stanton returns to save the crazed girl because it is the proper thing to do. Jim does not do the proper thing when he jumps from the Patna, and whether his suicidal return to Doramin and abandonment of Jewel is the proper thing is one of the most important, and enigmatic, questions raised in the novel.

The French Lieutenant comments that “an honest man...would confess that there is a point...when you let go everything...And you have got to live with that truth....Given a certain combination of circumstances, fear is sure to come’” (89). Despite the circumstances and despite this fear, the seaman must still adhere to a heroic code of conduct. The French Lieutenant seems on the verge of recollecting an anecdote concerning the trying of his own courage when he hastily concludes that one does not die of fear, but that loss of honor is a form of death. He condemns Jim for not performing his duty, as does Captain Brierly, another heroic foil and double of Jim, who participates in the pattern of descents, and considers the loss of honor worse than death. Brierly identifies with Jim as Marlow does, but also recognizes the inefficacy of life without honor as the French Lieutenant does. Guerard attributes Brierly’s destruction to excessive sympathetic identification with Jim. Marlow attributes Brierly’s destruction to “one of those trifles that awaken ideas—start into life some thought with which a man unused to such companionship finds it impossible to live” (36). Jim’s Eastern bride is a potential for heroism and
honor. Brierly’s bride, or companion, is the idea of his own loss of honor, a matter “of the gravest import” (36). He chooses to die at the peak of his honorable career rather than to risk losing his honor through some development of circumstances; Jim chooses to die rather than to lose what honor he has regained in Patusan.

While Jim’s descents begin with a leap from the Patna and end with his walk towards Doramin, Brierly jumps “overboard at sea barely a week after the inquiry...as though on that exact spot in the midst of waters he had suddenly perceived the gates of the other world flung open wide for his reception” (36). Brierly’s submersion, another example of the recurrent motif of descent into an “other world,” is triggered by Jim’s descent on the Patna. Brierly attends Jim’s trial as part of the panel passing judgment on Jim, and soon after passes judgment on himself. Brierly’s discomfort with the proceedings of Jim’s inquiry leads to a consultation with Marlow about Jim. Brierly feels Jim’s situation brings shame to the craft, offers financial aid to help Jim leave, and expresses anger that Jim has allowed the inquiry to torture him in this way.

While his interest in Jim’s fate aligns Brierly with Marlow, his identification with Jim and subsequent self-destruction associate him more closely as a double of Jim. Despite his “good-natured and contemptuous pity” of Marlow (36), the latter admits that there is something “indefinite and attractive” about Brierly (36). Similarly, Marlow is attracted to Jim because of his youthful appearance and despite Jim’s fierce egoism. Brierly, like Jim, turns his back on his duty to recover his honor and preserve his heroic image of himself as “Montague Brierly in command of the Ossa” (36). The Ossa is “the crack ship of the Blue Star line” (35) and Big Brierly, at thirty-two, about ten years senior to Jim, “had saved lives at sea, had rescued ships in distress [as did the French Lieutenant], had a gold chronometer presented to him..., and a pair of binoculars with a suitable inscription from some foreign Government, in commemoration of these services” (35-36). Marlow comments that “meek, friendly men” (36) did not usually like Brierly because of his sense of superiority. The image of superiority is what Brierly dies to save.
Brierly’s gray-headed mate shares the details of the night of Brierly’s descent with Marlow. The mate regrets his dislike for Brierly as he recounts the latter’s meticulous care of his ship before his ritual suicide (which foreshadows Jim’s). Brierly—like Marlow and Stein—is also a writer. Brierly records his own demise and he writes the letter to the mate giving instructions regarding the ship’s passage and hints at how to gain command of the Ossa. Brierly charts the fate of the mate of the Ossa with an eloquent letter to be delivered to the Company after his death. Brierly precisely lays down the chart and time “in his neat figures” (37), and instructs the mate, “Thirty-miles more as she goes…and then we shall be clear, and you may alter the course twenty degrees to the southward” (37). The mate, who does not understand Brierly’s exaggerated concern with such details at the time, inherits Brierly’s duties and his dog. Brierly sets the log for his mate, hangs his gold chronometer under the rail, places four iron belaying-pins from the mainmast in his pockets to help him down, and goes over the rail. The gold chronometer marks the spot where time stops for Brierly when he makes his artistic descent, just as time stops for Jim when he descends from the Patna. Like Stanton and the French Lieutenant, Brierly is utilized in the novel to explore the codes defining heroism, and the example of these three men is part of Conrad’s attempt to move the idea of heroism in the direction of artistry; ironically, though, the most artistic of these three heroes is the one whose suicidal course of action (doubling Jim’s) on the surface seems to offer the least potential for a future reinvention of those codes and for any ascent from the abyss of an unheroic underworld back into the clear light of day that the maritime code once seemed to offer a man like Brierly and for which Conrad still seems to hold out some ambivalent hope in Lord Jim.
Having given this synthetic account of how the code of honor functions in the narratives of three heroic doubles in Lord Jim, we can return to Patusan and to the last double of Jim: Gentleman Brown. Brown is an egoist who comes straight out of a Romantic tale of South Sea pirates, and one who does what he can to destroy Jim. In the lengthy written tale with which the novel closes (appended to a letter to an unidentified narrator), Marlow resurrects Brown just as he resurrects Jim. After describing a visit to Stein and the ghostly-grieving Jewel, Marlow’s “letter proper ended” (214) and the story of Jim’s final days begins on pages separate from the letter: “It all begins...with the man called Brown” (214). Marlow’s letter introduces Brown as a legendary Romantic figure, like Jim. Brown’s origin is obscure: “he was supposed to be the son of a baronet” (214). Like Jim, he is one about whom stories are told: “he was always trotted out in the stories of lawless life” (214). What distinguishes Brown from “his more celebrated prototypes” like Bully Hayes and Dirty Dick is “the arrogant temper of his misdeeds and a vehement scorn for mankind at large and for his victims in particular” (214). Brown is described as “savage and vengeful” even “in the days of his greatest glory” (215). The climax of Brown’s Romantic tale is the death of his lover: Marlow recounts Brown’s “sombre and violent grief” (215) over the young girl’s body as “the most wonderful part of the tale” (215). After this loss, Brown’s luck changes and he is driven in desperate straits into the storybook world of Patusan. Gentleman Brown is a Romantic figure in a tale, dead before the tale is told, just as Jim is. The similarities do not stop there.

Brown’s loyal Solomon Islander servant is described as a devil with “glittering eyes” (216); the loyalty and efficiency of the Solomon Islander recalls Tamb Itam’s faithful adherence to Jim. While Jim battles the “Dark Powers” to escape his past failure, Brown battles “an adverse
fortune” (215); both men are motivated by an “inconceivable egoism” (239), by “some complex intention” (214). By the time he reaches Patusan, Brown is, like Jim, “tired of his life, and not afraid of death” (216). Jim is imprisoned by his own memory and creates his own prison in Patusan; Brown “stood in mortal fear of imprisonment… the sort of terror a superstitious man would feel at the thought of being embraced by a spectre” (216). Jim embraces the specter of his honor. Desperation drives both men to Patusan. Brown is “running away from the spectre of a Spanish prison” (217), when he attempts to raid Patusan; Jim is fleeing his own dishonor. Like Jim, Brown survives because he surprises the Rajah’s stockade. In negotiating with Brown, Jim is seduced into what Albert Guerard defines as self-destructive identification with the desperate pirate. Identifying with Brown destroys Jim, just as identifying with Jim destroys Brierly. Jim cannot “tolerate the presence of his other self, Gentleman Brown, …[in]… the jungle village to which he [has] fled in quest of a new life far from constant reminders of his past” (Andreach, 58).

Jim’s identification with Brown begins when Brown tells Jim, “we are both dead men, and let us talk on that basis as equals” (232). Brown then evokes “an assumption of common experience; a sickening suggestion of common guilt, of secret knowledge that was like a bond of their minds and of their hearts” (235). This association with guilt, secret knowledge, and seductive speaking renders Brown Satan-like.

Marlow introduces Brown in Chapter 37 as a demonic figure gloating on Jim’s destruction upon his deathbed: “I did come upon him a few hours before he gave up his arrogant ghost” (209). Marlow must meet Brown’s gaze, “bear the sunken glare of his fierce, crow-footed eyes” (209), and hear Brown’s confession, if he wants to know how Brown destroyed Jim. In the following chapter, Marlow compares Brown to “some man-beast of folk-lore” (226), who “running his appointed course, … sails into Jim’s history, a blind accomplice of the Dark Powers” (215). Marlow defines Brown’s egoism as evil and insane: “Certain forms of evil are akin to madness, derived from intense egoism, inflamed by resistance, tearing the soul to pieces” (209). About Jim, Brown says, “he hadn’t devil enough in him to make an end of me” (209).
Brown’s gaze, “yellow eyes out of a long, ragged, brown face” (209), seems canine. The dying Brown is sheltered by “a loafing, fuddled vagabond—a white man living amongst the natives” in a hut with an obese Siamese woman who chews betel in a corner (reminiscent of Doramin’s wife). An unattractive little Buddha, “an ugly, yellow child, naked and pot-bellied like a little heathen god” (210), studies Brown’s dying Satanic form and provides a subtle link between Lord Jim and Heart of Darkness, in which Marlow is the Buddha-like figure telling the tale of Kurtz’s death. Marlow’s presence at the deathbed of Kurtz and the deathbed of Brown links the two characters from the two novels. In fact, a fragmented Kurtz appears in Lord Jim, in the double figures of Jim—supposedly benefiting the natives—and Brown—attempting to exploit them. Deborah Guth discusses Kurtz’s “Promethean quality” in Heart of Darkness. Brown’s insanely selfish greed contrasts with “the heroic gift of self that is the cornerstone of the Promethean myth” (Guth, 161); yet this “Promethean quality” applies both to Jim and to Brown. Jim and Brown are foils and doubles: Jim reflects the suffering self-sacrifice and Brown reflects the anger of Promethean transgression (“Like the ancient hero he is a symbol of daring and transgression, a lone forerunner,” Guth notes, “reflecting through his extreme suffering the anger of the powers he has defied”). Prometheus and Satan are both isolated and disobedient mythic archetypes or rebels. Guth compares Kurtz to Lucifer; Brown is described by Marlow as a devil. Brown certainly destroys the Romantic balance of life in Patusan much as Satan destroys paradise.

Dying, demonic Brown turns artist, confessing to Marlow his own tale of Jim’s destruction. Like Jim, Gentleman Brown is both art (narrated) and artist (narrator); he descends into and emerges from the underworld of Patusan in order to maintain an ideal image of himself, yet unlike Jim, Brown is not Christ-like but Satanic, aligned with the “Dark Powers” that confront Jim. Like Marlow and Jim, Brown is compelled to tell his tale: “He talked feverishly; but in the middle of a word...an invisible hand would take him by the throat, and he would look at me dumbly with an expression of doubt and anguish” (210). Brown’s narrative, like Marlow’s and Jim’s, is a necessary confession. He is compelled to tell his tale: “He seemed to fear that I would
get tired of waiting and go away, leaving him with his tale untold, with his exultation unexpressed” (210). Like Marlow, Brown resurrects Jim in his confessional narrative; like Jim, Brown is compelled to confess to Marlow.

Joseph Dobrinsky has argued that Jim, Marlow and Stein are the novel’s three primary protagonists who double each other, but his argument fails to take into additional account the fact that Brown is the dark double of all three. Brown is a crucial figure in the mythic substructure of the novel and in Conrad’s sacralization of the artist. Like Stein, Brown lost a young and beautiful love. Like the typical demon-lover archetype, Brown seduced the “wife of a missionary, a very young girl from Clapham” (215), away from her husband and to an early death; she dies soon after boarding Brown’s ship. Brown’s fierce antagonism towards Jim echoes Marlow’s distaste for Jim during their first interview. Like Jim and Stein, Brown is a legendary Romantic figure. Guerard’s discussion of Jim’s fatal identification with Brown emphasizes the latter’s role as Jim’s double. Though at times he faintly echoes Marlow, Brown strongly doubles both Jim and Stein, perhaps because more explicit mythic undertones construct his character. Brown’s artistry is not restricted to tale-telling and writing like Marlow’s artistry; Brown both tells his tale and lives his Romantic vision of himself, much as Jim and Stein do. While Jim creates a world, Brown—Miltonic in his rage and isolation—causes Jim to fall and destroys the world Jim has created. Brown's destruction of this world and of Jim subverts the efficacy of Jim's dream and his function as a Christ-like figure. Jim’s self-sacrificing death as a result of Brown’s treachery lacks the strong redemptive resonance of Christ’s sacrificial death.

All four characters—Jim, Marlow, Stein, and Brown—as both artists and mythic archetypes, participate in the novel’s pattern of descents and returns. In their roles as artists these characters double each other and the various mythic archetypes they evoke reinforce and echo one other to strengthen the mythic substructure of the novel. These doubles represent the dead and resurrected gods of the various descents and multiple underworlds of Lord Jim. While Jim, Brown, and Stein evoke one vegetative god or another—Christ, Satan, and Hades respectively—Marlow, like
Orpheus, descends and returns with a tale, while subtly doubling these more fertile, mythic figures.
As just stated, critics such as Dobrinsky and David Lynn have pointed out Conrad’s artistic triptych of Marlow, Stein, and Jim. Marlow, Stein, and Jim represent three disparate fragments of Conrad’s artistic identity, functioning as layered symbols of the quest for psychological or artistic maturity in Lord Jim (Lynn, 27). These three artists form a sacred if fragmented artistic trinity that echoes the minor trio of heroes—Stanton, the French Lieutenant, and Brierly—that I examined in the section on heroic codes of conduct. Stein, Marlow and Jim form an artistic triptych of the father, son and the Holy Ghost opposed by Brown’s Satanic form. In Orphic Stein, God and Hades meet. Marlow, solely Orphic, resurrects both Jim and Stein. Jim, both Orphic and Christian (predominantly Christian), both Romantic and modern, recreates a paradise for himself in Patusan after his Fall from the Patna—Brown destroys it.

As doubles, Stein and Marlow are both patriarchal figures guiding and then mourning Jim. For both Stein and Marlow, grief inspires art. Ghostly Stein has lost a wife and child and loses a son in Jim. Marlow’s voice is rendered hushed and distant as Stein’s in recounting his loss of Jim through the disruptions in his narrative. Stein, little more than a ghost, “a [R]omantic model who belongs already to a vanishing era” (Lynn, 37), waves farewell at the novel’s end, releasing the reins of master artist to Marlow. Marlow and Stein double each other and both also double Jim. Marlow evokes both Stein and Jim when he refers to himself paradoxically as a ghost recounting Jim’s tale: “and have I not stood up once, like an evoked ghost, to answer for his eternal constancy?” (253). Marlow’s life differs from Jim’s Romantic aspirations and achievements, while Stein has actually lived the life of a Romantic hero.
Stein's Romantic idealism has led him to Patusan, and he sends Jim along the same journey. In Patusan, a native befriends Stein. Like Jim and Dain Warris, Stein and his best friend, Mohammed Bonso "both became the heroes of innumerable exploits" (125). The natives recall these exploits for years afterwards. Stein, like Jim, inherits his role as trader in Patusan from a father-figure, an old Dutch traveler and trader, who leads the young Stein into the council-hall before the queen and declares Stein his son (125). Stein's tale of the princess's warning against his traveling alone and his successful defense against the ambushing assassins recalls Jewel's warning and Jim's defense against would-be assassins. Stein's dead princess and daughter link him to Jim by echoing Jewel and her dead mother. The ring that Stein gives to Jim is a sign to Doramin to treat Jim as he would Stein. When Marlow says goodbye to Stein in the few paragraphs after Jim's death has been chronicled, the reference to one dead Romantic hero implies the waning of the elder. Stein composes the final enigmatic image of Lord Jim as he "waves his hand sadly at his butterflies" (253). Stein, like Jim, has been resurrected through Marlow's Orphic tale, and Stein, like Jim, must be left behind in the world of shades.

Dobrinsky posits Stein as the "Conradian exemplar of the artist, in the nature of his gift, his devotion to his work, the inner springs of his vision, his specific mode of utterance, and the enviable strength achieved in the process" (33). Stein is a gifted explorer "whose cryptic pronouncements Marlow has journeyed far to hear and act upon" (28). Marlow defers to Stein as to a master artist until the end of the novel when Stein retires with Jewel in a house of shades. The mature Stein has metamorphosed from the young and Romantic adventurer and colonial exploiter to the sedentary and objectively distanced oracular speaker and artist. Stein is a Romantic figure who has led a heroic life and made the descent of the mythic hero into Patusan/Hades, where a heroine—the princess—served as the agent of life and death. Like Orpheus, Stein emerges from the underworld without his mate and having lost his virility. A "shadow prowling amongst the graves of butterflies" (130), Stein emerges to a death in life similar to Jewel's. After leaving Patusan, Stein's "tall form, as though robbed of its substance,
hovered noiselessly over invisible things with stooping and indefinite movements” (130). As an artist or writer, Stein is thus identified with Hades, a keeper of the dead who is described with demiurgic undertones. There is no place in the modern world for Stein’s Romanticism, anymore so than there is for Jim’s. Both characters belong to the subterranean realm to which Conrad’s Orphic artist descends to dig for the roots of mankind’s sense of wonder.

Dobrinsky’s analysis of Conrad’s artists in The Artist in Conrad’s Fiction: A Psychocritical Study recognizes Marlow, Jim, and Stein as the three primary protagonists and symbolic artists in Lord Jim, and usefully comments on Stein’s role in the novel; however, in addition to neglecting Gentleman Brown’s anti-heroic art of destruction, Dobrinsky also fails to take into account Stein’s passing of the reins to Marlow. In ignoring the arresting voice of the Satanic and withering artist Brown and Marlow’s ascendance to master artist, Dobrinsky fails to address the full scope and function of the mythic substructure of Lord Jim. Like Stein and Jim, Brown belongs to a world of Romantic adventure tales that cannot last and evokes the mythology of the slain and resurrected gods. Brown’s bitter rebellion against mankind evokes Stein’s parable about the man who struggles against, rather than immersing himself in, his destructive element. Brown never seeks renewal—his art is destruction and self-destruction. Brown is the destroyer, the angry god who slays himself. Stein is a Romantic and a dying shade, a slain god; Jim also is a slain god, Romantic and Christian—out-dated and inefficacious. Marlow is the Orphic artist resurrected in their stead.

Dobrinsky accurately depicts Marlow’s initial disciple-like subordination of his artistic ability to that of Stein, because Marlow acknowledges the stronger focus, better judgment, and experience of a master artist in Stein. Marlow describes Stein’s ability to see beyond the mortal, commenting on

the intense, almost passionate absorption with which he looked at a butterfly, as though on the bronze sheen of these frail wings, in the white tracings, in the gorgeous markings,
he could see other things, an image of something as perishable and defying destruction as these delicate and lifeless tissues displaying a splendor unmarrred by death. (126)

Marlow attributes this Romantic image-vision to both Stein and Jim, but never to himself; he explicitly denies that he possesses any imagination. Though the white tracings and the gorgeous markings of Stein’s butterfly have been translated by some critics as a metaphor for the written page, the focus of the passage is nonetheless Stein’s recording of his Romantic vision. Stein’s Romantic vision enables him to see more than what is there and to live according to his Romantic image of himself. Unlike Jim, Stein can look beyond himself to see that image in others. In Jim and in the other specimens he collects, Stein sees the image defying destruction, unmarrred by death. This image Stein catalogs and collects and describes in writing, much as Marlow does despite his lack of Romantic experience. Jim is captured in death, by both Stein and Marlow, as an image defying destruction and unmarrred by death.

While Marlow denies that he possesses such vision, he too is a re-collector of souls in the name of art. Marlow recollects and calls up ghosts, accepts confessions, consults with priests, and tells elegiac tales. Marlow does not record what he imagines Jim to be, but what he sees, in an effort to make his audience see Jim. Instead of imagination, Marlow attempts to perceive truth. Marlow’s repeated attempts to scrutinize Jim reiterate the younger man’s inscrutability and result in a catalog of images fraught with the rhetoric of enigma. His elegiac tales contain the images of perfect specimens defying destruction and unmarrred by death, recorded, passed on, like Stein’s insects (in a process of cataloguing that is, notwithstanding its Romantic genealogy, ironically complicit with the modern “order of things” being institutionalized through nineteenth-century scientific discourse). Marlow may praise Stein’s vision but the reason Marlow defers to Stein’s artistry in Jim’s case is actually Stein’s experience—Stein has been the Romantic hero and lived his vision. In the subterranean gloom of his home, Stein rescues a fragment of truth (to recall Conrad’s Nigger Preface) concerning Jim’s nature. The air of hushed sanctity that surrounds
Stein’s work and utterances conveys Marlow’s reverence for Stein and Conrad’s reverence for the artist as the true Conradian hero in Conrad’s modern mythology.

Together, Stein’s reverence for Nature as the great artist and Marlow’s reverence for Stein sacralize the role of the artist, even though neither Nature nor Stein can survive the transition into the modern world from which Marlow is compelled to write, and rewrite, them. Carrying his specimen in a glass case “religiously to its place, passing out of the bright circle of the lamp into the ring of fainter light—into shapeless dusk at last” (130), Stein recedes into the darkness much as Marlow describes Jim doing. It is significant that Marlow takes the question of Jim’s survival to Stein, to an artist. Marlow’s narrative posits Jim’s loss of honor and of the Romantic as “the great evil” for which he and Stein together must find “a practical remedy” (131). The great evil for which Marlow must actually find a remedy, however, is the evil of modernity, and Stein cannot guide him in this. If codes of conduct, values and belief systems are relative, how is modern man to define his existence and satisfy his needs for wonder and for order? Another great evil in *Lord Jim* seems to be the conflict of the Romantic (the hero that Jim—and maybe Marlow, vicariously—wants to be) and the modern (the consciousness that denies the possibility of such heroism). The novel’s encounter with the modern and its discovery of Modernism—fraught with “the waning of certainty, the fading of vision, the absence of final truth” (in Ian Watt’s words)—produce and chronicle the existential dilemma of how to be.

Stein’s final words dramatize the absence of final truth: “There were things, he said mournfully, that perhaps could never be told” (130). He certainly cannot tell Marlow the answer to the modern dilemma of how to be. Marlow, too, offers no remedy to the modern dilemma—except for a tale that repeatedly indicates the importance of the storyteller in conveying and grappling with this dilemma. Despite the inefficacy of language to communicate the mystery behind the veil of the visible world, Conrad still reverences the weaving of words in the passionate effort to produce truth.
The power of art, of the word, both spoken and written, is a central theme in *Lord Jim*. The power of words to resurrect and to destroy is inherent in *Lord Jim*'s patterns of descent and return and in the primary triptych of artists. Because Marlow is first described in the third person, then becomes a first-person narrator, he too seems to be brought to life by the original unidentified narrator of the text. In this way, Marlow himself is resurrected and then becomes a resurrector. His elegiac text resurrects a series of mythic doubles of himself and each other. Marlow remarks on the power of his words to influence Jim’s fate: “I had a sense of responsibility. If I spoke, would that motionless and suffering youth leap into the obscurity?” (106). “There is a weird power in the spoken word” (106), Marlow notes, while in the process of writing letters that will decide Jim’s fate; “And a word carries far—very far—deals destruction through time as the bullets go flying through space” (106), he adds. The power of Marlow’s spoken and written words effectively resurrects Jim, decides Jim’s fate, but also destroys Jim. Marlow’s words become Doramin’s bullets, killing the hero off in an enigmatic gesture of resurrection.

The exploration of Jim’s heroic dilemma may begin and end in a “persistently inconclusive and interrogative note” (Watt, 310), but the narrative consistently points attention back to Marlow’s art of weaving words. Marlow’s artistry includes the oral and written tale that resurrects and destroys Jim into a hero of sorts. When telling the tale of Jim, “Marlow’s body, extended at rest in the seat, would become very still, as though his spirit had winged its way back into the lapse of time and were speaking through his lips from the past” (21). Marlow’s text functions as the Orphic song to bring Jim/Eurydice back from the past and into the light for close scrutiny. Close scrutiny of the Romantic is fraught with paradox, as in the case of Patusan, the Romantic land that must be out of focus because it cannot sustain modern scrutiny. Patusan is part of that lonely region of stress and strife where Jim goes to make his appeal to the subtle and invincible solidarity that binds together the dead to the living. Marlow has known the living Jim but is now on a quest to call forth the dead Jim. Marlow’s text/song opens the underworld and sustains this opening as it disjoints time to resurrect an image of Jim. Marlow calls his own
narrative, “an unhealthy curiosity...the laying of what is the most obstinate ghost of man’s creation...more chilling than the certitude of death” (31); this Orphic narrative leads forth the ghost of Jim while simultaneously obscuring him. Marlow’s oral tale resurrects Jim, but his written account records, like Stein, Jim’s death. Marlow ascends from Patusan and from the underworld of Stein’s home, but he is forever locked in his own text, in the creation and loss of Jim, in the sacred weaving of words that order the chaos—in the Orphic dilemma.
In Lord Jim’s series of confessions—indicative of the sacred and necessary function of tale-telling as truth-producing—Marlow is both compelled to confess to characters like the French Lieutenant and to Stein, and he is sometimes reluctant confessor for a number of characters. Marlow first receives the confession of the engineer of the Patna, then Jim’s confessions in the Malabar House and in Marlow’s room. Brierly’s interview and subsequent suicide is a form of confession. Brierly’s subordinate from the Ossa confesses to Marlow, and Brown also confesses to him from his deathbed. Confessions are rituals evocative of religious redemption. Because of the Christian undertones, the ritual of confession reiterates the mythic substructure of the novel and reiterates as well the theme of the artist as a producer, or weaver, of truth.

Michel Foucault, in his History of Sexuality, describes the dynamics of confession as reconstitution, as a “production of truth” (Foucault, 65) and a constitution of subjectivity. “The confession,” he states, “is a ritual discourse in which the speaking subject is also the subject of the statement” (Foucault, 61):

It is also a ritual that unfolds within a power relationship, for one does not confess without the presence...of a partner who is not simply the interlocutor but the authority who requires the confession, prescribes and appreciates it, and intervenes in order to judge, punish, forgive, console, and reconcile; a ritual in which the truth is corroborated by the obstacles and resistances it has had to surmount in order to be formulated; and finally, a ritual in which the expression alone, independently of its external consequences, produces intrinsic modifications in the person who articulates it.... (Foucault, 61-62)

The modifications in the interlocutor of a Christian disposition involve redemption and self-constitution. Both Jim and the engineer suffer from guilt and desire some form of redemption.
Brierly wants to redeem faith in the honor of his profession and reputation. The first mate of the *Ossa* confesses to Marlow out of guilt over misjudging Brierly. Brown confesses to Marlow for purposes of exultation rather than redemption. Marlow confesses to the “priest”-like French Lieutenant in an effort to redeem Jim, and to the reader in an effort to make the reader understand Jim.

Through these acts of confession, the tale gains more truth—or at least the appearance of it—and yet at the same time more subjectivity. The subjectivity of the confessing character is reconstituted and truth is affirmed and produced. Marlow’s own tale is in this way corroborated and his subjectivity confirmed. When one character is compelled to confess, the interlocutor is compelled to comprehend, to understand, especially in the case of Marlow and Jim. The reader is likewise compelled according to the ritual of confession to understand Marlow and the tale he confesses, even though this understanding opens the reader up to a truth that is ultimately “unchartable.” The subjectivity of each successive confessor is at the heart of Conrad’s impressionism, undermining any objective reality or interpretation of the series of events that determine Jim’s fate, and yet forcing us—both consciously and unconsciously (Frederick Karl notes that literary impressionism uses verbal modes that “are connected to the release of the unconscious” [133])—to participate in the reality of the confessor’s subjectivity. Conrad draws the reader into his text as a participant, the interlocutor who hears a series of confessions, including Marlow’s, and whose final judgment of Jim will be determined by both conscious and unconscious variables that are secreted by Conrad’s enigmatic text.

Marlow’s ambivalent feelings about Jim’s Romantic condition are reflected in his “struggle to understand and to communicate” (Fraser, 42), to absorb and to recount Jim’s confessions and tale:

One of the reasons for the interrogative and retrospective aspects of Marlow’s narration in *Lord Jim* is the duty imposed upon Marlow by Jim to ‘understand,’ and the more Marlow demonstrates his struggle to comprehend, the more clearly the reader perceives his commitment. Thus, Marlow tells us that “I cannot say that I had ever seen him
distinctly—not even to this day, after I had my last view of him; but it seemed to me that 
the less I understood the more I was bound to him in the name of that doubt which is the 
inseparable part of our knowledge.” (Fraser, 42).

Like Marlow, the less the reader easily understands about Jim, the more the reader is similarly 
bound in solidarity to try to do so. Likewise, the less the reader understands Marlow, the more he 
is bound to attempt to do so. Marlow and Jim form a composite hero amid a complicated 
overlapping of doubles. To understand one, the reader must understand the other—indeed, all the 
others, who in contradictory fragments reflect an heroic self that can never again be viewed 
whole.

The moral chaos of the modern age fragments the modern identity, disassembling and 
isolating the heroic self; can these fragments of identity be reassembled, and solidarity be 
renewed? Ian Watt poses these questions when he argues that Lord Jim represents, through “the 
tale of friendship” (Watt, 336), the fragmentation of the modern age. In Jim, Watt sees the youth 
of a civilization and in Marlow he sees the experience of the modern age. Watt defines the 
friendship between Jim and Marlow as dominated by “elements of separateness, incompleteness, 
and misunderstanding which are reflections not only of the personal idiosyncrasies of Jim and 
Marlow but of some of the characteristic social and intellectual divisions of the modern world” 
(Watt, 336). Watt acknowledges that Conrad’s impressionist presentation of Jim and Marlow in 
Lord Jim forces the reader to participate “in its existential realities, realities which are so 
distinctly representative of the difficulties and doubts of the modern [experience]” (Watt, 337). 
Lord Jim begins in the past tense and ends in the present tense, a “complex communion of youth 
and age” (Watt, 319). Jim is a mirror for Marlow, who is a mirror for the reader, and Conrad 
offers no conclusion to the mystery of existence other than asserting the need for solidarity and 
the sacred function of the artist in communicating this need, despite the divisions that his text 
must lay bare—divisions that do not, however, preclude moments of communion, and confession. 
When Marlow “fulfills the responsibility he assumed early on for Jim with a portrait capturing
without diminishing the contradictions of his character” (Lynn, 29), he also captures the contradictions of his own character, and of the modern character; it is this “responsibility” of self-portraiture (confession) through portraying others that may sum up Conrad’s efforts in *Lord Jim* at maintaining a positive (Romantic?) emphasis on solidarity in the face of the fragmenting experience of modernity.

Marlow himself is both Romantic and modern in the sense that he, like Conrad, is a modern artist in possession of a certain nostalgia for the Romantic tradition. Strauss notes in *Lord Jim* the “modern pathos of time and history” (Strauss, 13) and how it contrasts with the Romantic period’s “quest for the lost or forgotten self” (Strauss, 13). In resurrecting Jim, Marlow is resurrecting—confessing to—a lost, Romantic self, escaping time and history only to return repeatedly to that from which he is escaping. Marlow returns to Jim’s past (which is also his own) and then returns to his present, but exactly what Marlow returns with must remain questionable. Is the knowledge Marlow carries out of *Lord Jim* a source of renewal, or a burdensome, unspeakable vision about the absence of truth? Critics have given positive responses to both of these questions, but my own inclination has been to emphasize the first position, finding meaning in the heroic and artistic acts of creation in the novel, and in the enigmatic solidarity they make possible.

Commenting on Conrad’s *A Personal Record*, Gail Fraser gives a sense of this justification of the artist’s creation in positive as opposed to nihilistic terms, recognizing the sacred role of the artist in ordering the chaos of modern experience for mankind:

> the sole moral justification for a ‘spectacular’ world is to be found in man’s ‘unwearied self-forgetful attention to every phase of the living universe reflected in our consciousness,’ the task being ‘to bear true testimony’ actively and without despair.

(Fraser, 71)

Marlow’s tale is not characterized by despair but by the determination to make some meaning out of chaos and by the sacredness of such a purpose. “Confronting the mystery of being,” Andreach
notes, "constitutes a religious experience: the feelings experienced by the limited before the unlimited, before one's soul or that of another person" (Andreach, 49). Marlow's tale is his confrontation with the mystery of being. Marlow repeatedly implies that descent is necessary for the construction of his tale. Certainly, Jim's descents and death are necessary for his Romantic construction of himself and for the legendary quality of the construction of Marlow's tale. The artist must descend as the mythic hero does to face the death or meaninglessness in himself in order to construct a meaningful tale or existence out of this meaninglessness. Marlow descends and faces the chaos embodied by his past self, Jim, in an artistic gesture that David Lynn has fittingly described as "faint, private, and, nevertheless, heroic" (Lynn, 37).
(xiii) Conclusion: "Death of the Author" and Orphic Descent

One last word in conclusion. Lynn’s description of Marlow’s artistic gesture of confession is reminiscent in some ways of what Roland Barthes had to say in his essay “The Death of the Author.” In that essay, Barthes connects writing or recounting to death:

> once a fact is recounted—for intransitive purposes, and no longer to act directly upon reality, i.e., exclusive of any function except that exercise of the symbol itself—this gap appears, the voice loses its origin, the author enters into his own death, writing begins.

(Barthes, 142)

This statement is of obvious relevance to the pattern of Orphic descent in Lord Jim. By the tale’s end, “Jim dead and Patusan dismembered, each surviving only through the narrative, Marlow himself has become incorporeal, no longer even a voice in the darkness, but withdrawn to written testimony for a solitary audience” (Lynn, 37). The “facts” have been recounted, and Marlow disappears into the seams of his written narrative. Barthes calls writing “that neuter, that composite, that obliquity into which our subject flees, the black-and-white where all identity is lost, beginning with the very identity of the body that writes” (Barthes, 142). His argument is similar to that of Blanchot in “The Gaze of Orpheus” and also recalls Allon White’s discussion of the rhetoric of enigma, in which he argues that Jim only exists in the seams of Marlow’s narrative as an absence indicative of mystery—an absence that becomes visible through this act of recounting. Like Jim, Marlow also eventually becomes an absence indicative of mystery, lost in the obliquity of Conrad’s text.

The artist and narrator Marlow suffers the death of the author along with the rebirth of the mythic hero through the ritual reenactment of his tale, his link to mankind. Characters such as Jim and Brown become completely the other—Eurydices, slain gods who do not...
emerge from the darkness—and ultimately Marlow himself must “die” and become other to himself in order for this mythic recounting to happen. The artists in Conrad’s Marlovian trilogy *Heart of Darkness* and *Lord Jim* have the Orphic “power that causes the night to open” (Blanchot, 99) for the modern reader, who by meeting the gaze of the unknown, the gaze of Orpheus, may find death and death-in-life, but also redemption and rebirth—all of the contradictions of the modern experience, indeed, along with the promise of an enigmatic connection, “faint” but nevertheless “heroic,” to one’s fellow man.
Works Cited


VITA

Sonya Fay Willie

CIRCADIAN RHYTHMS AND MELATONIN RECEPTORS AS SOURCES OF INDIVIDUAL VARIATION IN REPRODUCTIVE PHOTORESPONSIVENESS

A Thesis

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Paul Heideman

Margaret Saha

Eric Bradley
DEDICATION

This work is dedicated to the memory of Baninder Taneja.

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Abstract

This study had two main objectives. The first pair of experiments was designed to describe the role of the circadian system as a potential source of individual variation in reproductive photoresponsiveness in the white-footed mouse, *Peromyscus leucopus*. The second goal of this study was to clone the *P. leucopus* melatonin-1a (Mel1a) receptor, a G-protein coupled receptor involved in the molecular pathway regulating photoresponsiveness in this species and other seasonally-reproducing mammals.

Circadian characteristics of locomotor activity were determined by housing both male and female responsive and nonresponsive mice in cages equipped with running wheels and exposing them to a photocycle of 9-10 short days (SD), 26 long days (LD) and 14 days of constant darkness (DD). Nonresponsive mice exhibited a significantly longer free-running period of locomotor activity in DD than responsive mice, due primarily to the lengthened tau of nonresponsive females. There were no significant differences between responsive and nonresponsive mice in duration or phase angle of activity in either SD or LD. In addition, there were no significant correlations between circadian rhythms and reproductive development in male mice from an unselected control line.

Young responsive and nonresponsive mice were housed in DD to determine the effect of removing a photoperiodic cue on reproductive development. Nonresponsive mice exhibited significantly larger paired testis weights, paired seminal vesicle weights, paired ovarian weights, uterine weights, and body weights after 45 ± 3 days of DD exposure than responsive mice. This result demonstrates that subtle differences in circadian rhythms between responsive and nonresponsive mice are not biologically relevant to the photoperiodic regulation of reproduction.

The *P. leucopus* Mel1a receptor was partially cloned by screening a *P. leucopus* genomic library separately with two fragments of the *Mus musculus* Mel1a receptor cDNA clone as a probe. The resulting phage DNA was isolated, subcloned and sequenced. One 2 kb *P. leucopus* clone contained DNA that was highly homologous to the second exon of Mel1a receptor sequences in all other species in which the gene has been cloned. Future studies will use the *P. leucopus* Mel1a receptor clone to study patterns of gene expression through in situ hybridization, RNAse protection assays, and RT-PCR.
CIRCADIAN RHYTHMS AND MELATONIN RECEPTORS AS SOURCES OF INDIVIDUAL VARIATION IN REPRODUCTIVE PHOTORESPONSIVENESS
CHAPTER ONE

Introduction

Seasonal reproduction in mammals

Mammals that possess heritable traits that enable them to survive and contribute their genes to the next generation will be favored by natural selection. Such traits, whether behavioral, physiological, or morphological in nature, allow mammals to withstand environmental pressures long enough to successfully reproduce. Factors such as food availability, rainfall, humidity, temperature, predation, and inter- and intraspecific competition act as environmental pressures that can determine the potential for survival and successful reproduction. Because the vast majority of environments inhabited by mammals exhibit some degree of seasonal variation in one or more of these pressures, most mammals synchronize their reproductive efforts to a particular time of the year when resources are sufficiently abundant for the development and rearing of offspring.

Mammals living in environments where there is seasonal variation in climate and food availability can adjust their reproductive efforts either by reacting directly to environmental change or using predictive environmental cues (Bronson and Heideman, 1994). Species that react directly to environmental fluctuations in climate and food availability will attempt to reproduce depending on short-term environmental conditions. Others detect environmental cues that predict oncoming periods of time when food availability and climate will permit successful reproduction. The use of cues allows mammals to prepare metabolically for seasonal change and time reproductive events to occur during optimal environmental conditions. The best-known predictive cue exploited
by mammals is photoperiod, a cue that can serve as a precise reference for the time of year (Bronson and Heideman, 1994; Nelson, 1995).

**Photoperiodic regulation of reproduction**

Daylength, or photoperiod, is the primary environmental cue used by mammals to regulate reproduction on a seasonal basis. Annual change in photoperiod occurs in non-equatorial environments and provides a remarkably reliable cue for mammals to use to determine the time of year and make advance physiological adjustments. A decrease in photoperiod, indicative of the onset of winter conditions, can cause gonadal regression and cessation of reproduction in a variety of rodent species (reviewed in Bronson and Heideman, 1994). Mammals sensitive to photoperiod are thought to fall into two distinct categories: (1) those that exhibit endogenous circannual cycles of reproductive activity that are synchronized, or entrained, to seasonal changes in climate and food availability by photoperiod; and (2) those that fail to exhibit an endogenous rhythm of reproductive activity in the absence of environmental cues and use photoperiod to either initiate or terminate gonadal activity (Bronson and Heideman, 1994; Elliott and Goldman, 1981; Nelson, 1995).

To date, there are only a few documented cases of mammals that use photoperiod to entrain an endogenous circannual rhythm of reproduction to environmental cycles of climate and food availability (see Gwinner, 1986 for review). Kenagy (1980) showed that ground squirrels maintained an endogenous rhythm of testis size when placed under constant daylength. Goss and colleagues determined that deer exhibited a circannual rhythm of reproductive activity when exposed to photoperiods of less than 12 hours
By far, the sheep is the most well characterized photoperiodic mammal that uses photoperiod to entrain an endogenous reproductive cycle. Karsch et al. (1984; reviewed in Bronson and Heideman, 1994) determined that ewes exhibited recurring cycles of hormone levels when maintained under prolonged exposure to an 8L:16D photoperiod. Experimental evidence suggests that long day photoperiods act to bring the ewe’s reproductive cycle in phase with the annual cycle of food availability and with the other ewes in the population, while short day lengths lengthen the period of the endogenous rhythm to one year (Bronson and Heideman, 1994).

Most photoperiodic mammals display endogenously timed changes in reproductive function in response to a decrease or increase in photoperiod (Elliott and Goldman, 1981). When exposed to constant laboratory photoperiods in which lights on and off are abrupt, these mammals detect a ‘critical’ daylength that can either initiate or terminate gonadal activity. For example, the Syrian (Golden) hamster, *Mesocricetus auratus*, uses this strategy to terminate gonadal development when the photoperiod falls below 12.5 hours of light per day (reviewed in Bronson and Heideman, 1994; Nelson, 1995). After 4-5 months of treatment under a short photoperiod, hamsters enter a photorefractory state in which they are no longer suppressed by short day lengths and undergo spontaneous gonadal recrudescence. In the wild, photorefractoriness could allow hamsters and other mammals sensitive to photoperiod to become reproductively active in late winter/early spring before daylength surpasses the critical photoperiod. Such a strategy might be adaptive for rodents in that lactation, the most energetically demanding
stage of the female reproductive cycle, will coincide more precisely with the first flush of
vegetation growth in the spring (Bronson and Heideman, 1994).

Experimental evidence indicates that mammals do not just measure absolute
daylength, but compare the present daylength to a previous daylength, in order to
determine reproductive state. For example, the reproductive photoresponse of the
juvenile vole, *Microtus montanus*, to short day lengths, depends on the photoperiod that
preceded it: animals raised in short days were stimulated by longer day length, while
animals raised in long days were repressed by short days (Horton, 1984). A similar effect
of photoperiodic history has been documented in Siberian hamsters (Gorman and Zucker,
1997; Stetson et al., 1986) and can also be transmitted in utero in voles (Horton, 1985;
Lee et al., 1987). Thus, it appears that both the absolute photoperiod length and the
direction, or rate, of the change in photoperiod length determine reproductive state in mammals.

It is evident that mammals can use photoperiod to synchronize reproductive cycles
to the changing seasons. Photoperiodic mammals must somehow interpret the amount of
light per day and relay this information to the central nervous system in such a way that it
stimulates or represses the reproductive system via the hypothalamic-pituitary-gonadal
(HPG) axis. The circadian system plays an important part in photoperiodic time
measurement and the eventual reproductive adjustments caused by changes in daylength.

**The circadian system and photoresponsiveness**

In theory, temporal regulation of reproduction by environmental light cycles must
involve a physiological system that can accurately measure daylength and send a signal to
the HPG axis to trigger the appropriate reproductive response. It has been established that the circadian system is involved in photoperiodic time measurement (PTM) in mammals. The circadian system is responsible for generating oscillations in behavioral and biochemical processes that cycle over a period of approximately 24 hours. Circadian rhythms become entrained to a 24 hour cycle by environmental signals, generally light, but will persist in the absence of such cues. Rhythms are said to ‘free-run’ in the absence of cues and will display a free-running period ($\tau$) greater or less than 24 hours. The free running period of an organism’s circadian system determines how it entrains to a given light cycle and may affect its reproductive response to photoperiod. In mammals, the suprachiasmatic nuclei (SCN) of the anterior hypothalamus are necessary for the generation of circadian rhythms (Takahashi, 1995). Studies have shown that SCN ablation abolishes circadian rhythms of locomotor activity, feeding, drinking, sleep-wake, body temperature, and hormonal release (Moore and Eichler, 1972; Refinetti et al., 1993; Schwartz and Zimmerman, 1991; Stephan and Zucker, 1972; reviewed in Turek and Van Cauter, 1994) and can eliminate reproductive photoresponsiveness (Bittman et al., 1991; Rusak and Morin, 1976; Stetson and Watson-Whitmyre, 1976).

**Entrainment of circadian rhythms by light**

The principle entraining agent for mammals, birds, and most other organisms is light, while temperature can also have an effect, most notably in reptiles (Elliott and Goldman, 1981). Light acts to entrain the phase of a given circadian rhythm to occur during a particular time of day. For example, locomotor activity is a common rhythm used to study the circadian system of vertebrates. In mice and other nocturnal rodents,
activity occurs during the dark portion of a 24 hour cycle (see Figure 2). Activity begins shortly after light offset and may persist throughout the entire dark period. The duration of nocturnal activity (activity time, \( \alpha \)) is determined by the duration of the dark period: \( P. leucopus \) activity approximates 8 hours during a 16L:8D cycle and about 14 hours during an 8L:16D cycle (Figure 2). The activity rhythms of mice exposed to 24 hour light:dark cycles exhibit stable entrainment and the period of the activity rhythm (\( \tau \)) equals the period of the light cycle (\( T \)). Phase angle, or onset of the activity rhythm relative to either light onset or offset, is also stable, occurring shortly after lights off. Removal of light causes the activity rhythm to free run with a period either greater or less than 24 hours. Animals with \( \tau > 24 \) hours undergo phase delays, starting activity later each day, while animals with \( \tau < 24 \) hours undergo phase advances, beginning activity earlier each day. Tau, phase angle, and alpha are parameters that can be determined for a wide variety of rhythms, including neuropeptide levels, gene expression, body temperature, neuronal activity, and a variety of other processes regulated on a circadian basis.

Entrainment of circadian rhythms to light can be demonstrated by exposing organisms in constant dark to brief pulses of light at different circadian times (ct) and observing the presence or absence of a phase shift in the measured rhythm. By convention, activity onset for nocturnal animals is designated at ct 12 and marks the beginning of the subjective night (ct 12-24), while ct 0-12 is defined as the subjective day (Elliott and Goldman, 1981). The effect of light pulse exposure at different times of the day on the entrainment pattern of circadian rhythms is illustrated in Figure 1 (adapted from Elliott and Goldman, 1981). Light falling during the early subjective night causes a phase delay in which activity is delayed on the next day, while light exposure during the
late subjective night causes a phase advance, in which activity begins earlier on the following day. During most of the subjective day (ct 1-11), a ‘dead zone’ exists where light has no effect on the entrainment pattern of circadian rhythms.

**Photoperiodic Time Measurement**

Two competing hypotheses have been proposed to explain how organisms can measure photoperiodic time. The first hypothesis, dubbed the “hourglass” or “interval” timer model, proposes that a critical duration of light or dark, or a critical ratio of light:dark in each daily cycle determines the photoperiodic response of an organism (Elliott and Goldman, 1981). In this model, some photochemical process occurs during the light (or dark) cycle, resulting in the accumulation of a hypothetical reaction product. Long days (or nights) can cause accumulation of the reaction product to exceed threshold and stimulate a photoperiodic response (Elliott and Goldman, 1981). The hourglass timer does not exhibit circadian rhythmicity itself. Rather, the hourglass timer elicits its physiological effects on reproduction only after appropriate stimulation by the environmental light:dark cycle (Elliott and Goldman, 1981). Photoperiodic time measurement by an hourglass timer has been demonstrated in at least two insect species, the aphid *Megoura viciae* and the European corn borer *Ostrinia nubilalis* (Lees, 1966; Skopik and Bowen, 1976), and males of the iguanid lizard species *Anolis carolinesis* (Underwood, 1979).

The second hypothesis for photoperiodic time measurement involves a physiological timer that exhibits a circadian responsiveness to light. First proposed by Büning (1936; in Elliott and Goldman, 1981) to explain rhythmicity in plants, this
model assumes that an endogenous circadian rhythm of photoperiodic photoresponsivity (CRPP) enables the timer to be stimulated by light during only one half of its approximately 24 hour cycle. By convention, the half-cycle responsive to light is called subjective night, while the half-cycle nonresponsive to light is called subjective day. Photoperiodic stimulation occurs when light from long days impinges on the photoresponsive portion of the CRPP. Light from short days is restricted to the nonresponsive portion of the CRPP and cannot stimulate a photoperiodic response (Bünning, 1960; Elliott, 1976).

Two versions of Bünning's original hypothesis have emerged in recent years to explain photoperiodic time measurement. Pittendrigh and Minis (1964) adapted Bünning's hypothesis and proposed the external coincidence model of photoperiodic time measurement. In this model, light serves both to entrain the CRPP (and all other circadian rhythms) and can induce a photoperiodic response only when the photoresponsive half-cycle ($\phi_t$) is illuminated. Thus, temporal coincidence of light and $\phi_t$ is dependent on both the duration of light and the entrainment pattern of the CRPP to the light:dark cycle (Elliott and Goldman, 1981). The internal coincidence model, on the other hand, states that the phase relationship of multiple circadian oscillations determines photoperiodic time measurement. Essentially, physiological function of a particular process, such as reproduction, becomes altered when the phase of one circadian rhythm changes in relation to the phase of another oscillator as the organism entrains to a longer or shorter photoperiod. In this model, light serves to differentially entrain the multiple circadian oscillators of an organism, indirectly affecting physiological function when the phases of the rhythms change in relation to each other (Elliott and Goldman, 1981).
Evidence gathered from resonance cycle experiments described below suggests that mammals measure photoperiodic time through a circadian mechanism instead of the hourglass model seen in insects and lizards. The resonance experimental protocol typically involves exposing animals to exotic, non-natural light:dark cycles of 6 hours of light followed by a dark period that increases by multiples of 12 hours to give periods (T) of 24, 36, 48, and 60 hours. In other words, six hours of light repeats every 24, 36, 48 or 60 hours. Six hours of light is well below the critical photoperiod for reproduction in mammals. If mammalian photoperiodic time measurement is regulated by an hourglass model in which the absolute duration of daylength determines reproductive state, then all animals exposed to these light cycles will exhibit gonadal regression. If the circadian system is involved, then only animals exposed to photoperiods in which light falls at the same time during the subjective day of the CRPP (T = 24, 48) will exhibit gonadal regression. Resonance cycles with periods of (T = 36, 60) will induce gonadal development because light exposure alternates between the subjective day and photosensitive subjective night, resulting in long-day interpretation of the photocycle. Resonance experiments have determined that photoperiodic time measurement is regulated by the circadian system in Syrian hamsters (*Mesocricetus auratus*; Elliott, 1976), white-footed mice (*Peromyscus leucopus*; Sullivan and Lynch, 1986), deer mice (*Peromyscus maniculatus*; Whitsett et al., 1983), and voles (*Microtus agrestis*; Grococh and Clarke, 1974).

T-cycle experiments can also provide strong evidence that photoperiodic time measurement is regulated by the circadian system in mammals. The premise of this experiment is simple: a short light pulse administered every 24 hours should promote or
inhibit gonadal growth depending on the phase of the CRPP it illuminates each day.

Timing the light pulse to occur at the same circadian time each day is achieved by varying T, the period length (total length) of the entire light:dark cycle. The light pulse serves both to entrain the circadian system and acts as a photoperiodic stimulus (Elliott and Goldman, 1981). Pittendrigh (1965) devised the equation $\tau - T = \Delta \phi$ to predict the circadian time at which a light pulse from a given T-cycle would occur to produce a phase shift necessary for entrainment. For example, an animal that exhibits a free-running period ($\tau$) of 23.7 hours would phase delay activity -0.8 hours each day if exposed to a T-cycle with a period (T) of 24.5 hours ($23.7 - 24.5 = -0.8$ hours; negative values denote phase delays, positive values denote phase advances). This occurs because a 1-hour light pulse given every 24.5 hours would effectively fall during the early subjective night (near ct 12) every circadian cycle, causing the animal to phase delay each day and also stimulating $\phi$.

T-cycle experiments have demonstrated that many photoperiodic rodents measure photoperiodic time by a circadian mechanism. Elliott (1976) showed that male Syrian hamsters (*Mesocricetus auratus*) maintained large testes when exposed to T-cycle periods that differed from 24 hours by greater or less than 0.5h. However, gonadal regression occurred in hamsters exposed to T-cycles of periods that equaled 24 hours (and nearly equaled the period of their free-running rhythms). Similar effects on testicular development have been demonstrated in deer mice (Underwood et al., 1985), white-footed mice (Sullivan and Lynch, 1986), and Djungarian hamsters (Darrow and Goldman, 1985). Puchalski and Lynch (1994) used the T-cycle paradigm to demonstrate that non-photoresponsive Djungarian hamsters could exhibit gonadal regression typical of
photoresponsive hamsters by exposing them to T-cycle periods which approximated the period of their longer (>24h) free-running rhythms.

**Neuroendocrine regulation of reproduction**

*The hypothalamic-pituitary-gonadal axis*

Mammalian reproductive status is controlled by neuroendocrine activity along the hypothalamic-pituitary-gonadal (HPG) axis. Environmental stimuli is transduced and integrated into the central nervous system and may affect reproduction by synaptic input to gonadotropin releasing hormone (GnRH) neurons that project to the hypothalamus. GnRH is a highly conserved decapeptide hormone so named for its ability to stimulate the release of the gonadotropins leutenizing hormone (LH) and follicle-stimulating hormone (FSH) from the anterior pituitary (King and Millar, 1995). Immunohistochemical analysis of the rat brain has determined that there are approximately 1200-1400 GnRH-containing neurons distributed in a diffuse band from the olfactory bulb and related structures throughout the rostral hypothalamus, with cell bodies located in the medial, lateral, and triangular septal nuclei, the diagonal band of Broca (DBB), the bed nucleus of the stria terminalis (BNST), the suprachiasmatic nuclei (SCN), the medial and lateral preoptic nuclei, the periventricular nuclei (PeVN), the anterior hypothalamic nuclei, and the ventrolateral hypothalamic region dorsal to the supraoptic nuclei and olfactory tracts (Sagrillo et al., 1996; see Silverman et al., 1994 for a comprehensive review). Although these neurons send projections to a variety of brain regions near the rostral hypothalamus, including a major pathway to the organum vasculum of the lamina terminalis (OVLT), 50-70% of all GnRH neurons project to the median eminence (Sagrillo et al., 1996).
The significance of projections to the median eminence (ME) for reproductive function cannot be understated. The ME encompasses the base of the hypothalamus adjacent to the infundibulum, or pituitary stalk. It contains a capillary plexus that connects to the hypophyseal portal system, a closed circulatory loop that drains into the adenohypophysis, or anterior pituitary. Humoral messages secreted from the ME travel through the hypophyseal portal system and arrive at the anterior pituitary. GnRH neurons regulate anterior pituitary function by releasing GnRH from terminals in the ME, where it is picked up by the capillary plexus, circulates through the portal system, and binds to specific G-protein coupled receptors on the surfaces of pituitary gonadotrophs (Stojilkovic et al., 1994). The GnRH receptors stimulate a phospholipase second messenger pathway which causes an increase in intracellular calcium levels, ultimately resulting in an increase in synthesis and release of LH and FSH (Stojilkovic et al., 1994).

The importance of GnRH in the regulation of pituitary gonadotropin secretion is demonstrated by the mouse hpg mutation, a naturally-occurring, 33.5 kb deletion spanning exons 3 and 4 of the GnRH gene. Homozygous mutants exhibit no detectable levels of serum gonadotropins and completely lack gonadal development (Cattanach et al., 1977).

LH and FSH stimulate development of the gonads in mammals. Both are glycoprotein hormones that, upon release from pituitary gonadotrophs, travel through the systemic circulation and bind to receptors in the testes and ovaries. LH binds to high-affinity, membrane-bound receptors on Leydig cells of the testes to stimulate cell maturation and testosterone secretion. In the female, LH-receptor interaction on the surface of ovarian cells stimulates development of the follicles, ovulation, and estrogen
secretion. FSH binds to surface receptors of Sertoli cells in the testes to regulate spermatogenesis in males and aids in the development of the follicles in females (Griffin and Ojeda, 1992).

Clearly, mammalian reproductive status is dependent on hypothalamic release of GnRH. Control of GnRH secretion occurs through the various synaptic, endocrine, and autocrine inputs GnRH neurons receive in the brain. GnRH neurons receive synaptic input from afferent fibers containing norepinephrine (NE), dopamine (DA), serotonin (5HT), gamma-aminobutyric acid (GABA), glutamate, corticotropin-releasing hormone, substance P, neuropeptide Y (NPY), pro-opiomelanocortin (POMC), and β-endorphin (reviewed in Sagrillo et al., 1996; Silverman et al., 1994). The sheer number of different afferent inputs GnRH neurons receive likely reflect the importance of properly integrating many sources of sensory information for the regulation of reproduction. In addition, sex steroids and GnRH itself can negatively feedback to GnRH neurons to regulate GnRH secretion (Sagrillo et al., 1996). Many aspects of the neuroendocrine pathway in which photoperiod is measured have been determined and clearly implicate melatonin as the key hormonal factor in seasonal regulation of reproduction. However, the mechanism through which melatonin affects the HPG axis is not well understood.

Effect of daylength on reproductive status

The pathway in which photoperiod is integrated by the central nervous system has been well characterized (reviewed in Turek and Van Cauter, 1994). Retinal photoreceptors that detect light information independently from visual photoreceptors (Lucas and Foster, 1999) transduce a signal to the SCN via the retino-hypothalamic tract.
(RHT) (Moore and Eichler, 1972; Moore and Lenn, 1972; Stephan and Zucker, 1972a, 1972b). Efferent projections from the SCN innervate the paraventricular nucleus (PVN) of the hypothalamus, which in turn sends efferents to the intermediolateral nucleus of the spinal cord. Preganglionic neurons from this region send impulses to the superior cervical ganglion (SCG) in the neck. Beta-adrenergic fibers derived from the SCG travel above the third ventricle and synapse at the pineal gland, where they secrete norepinephrine (NE). The pineal gland, an endocrine effector organ of the autonomic nervous system, regulates reproductive state by producing and secreting the hormone melatonin. However, the importance of this entire neuroendocrine pathway is demonstrated by surgical manipulation: disruption of fibers between the SCN and PVN, or the PVN and any of the afferent and efferent fibers relaying messages to the pineal gland, abolishes reproductive photoresponsiveness (reviewed in Hadley, 1992; Turek and Van Cauter, 1994).

Binding of NE by β-adrenergic receptors on the surface of pinealocytes of the pineal gland causes an increase in the uptake of tryptophan. Activation of a cAMP second messenger pathway also occurs, resulting in the conversion of tryptophan to serotonin and then serotonin to N-acetylserotonin. The final product of this synthesis pathway is the indoleamine melatonin, which is secreted from the pinealocytes into the circulation. N-acetyltransferase (NAT) is the rate-limiting enzyme in the production of melatonin; NAT activity increases in response to NE stimulation (reviewed in Hadley, 1992).

The pattern of melatonin secretion has been thoroughly documented for many mammalian species and is entrained by the environmental light:dark cycle. Typically,
mammals exhibit a pronounced circadian rhythm of plasma melatonin levels, with nearly undetectable levels during the day that increases dramatically during the night (Turek and Van Cauter, 1994). The melatonin rhythm provides an endocrine measure of daylength: long duration melatonin pulses are characteristic of short days, and shorter bursts of nocturnal melatonin indicate long days. It is the duration of the nocturnal rise in melatonin that determines gonadal response to seasonal change in photoperiod. Long duration melatonin pulses characteristic of short days induce gonadal regression in many photoperiodic rodents, including white-footed mice (*Peromyscus leucopus*; Dowell and Lynch, 1987), deer mice (*Peromyscus maniculatus*; Blank and Freeman, 1991), and Djungarian hamsters (*Phodopus sungorus*; Carter and Goldman, 1983). Surgical ablation of the pineal gland results in the disappearance of the melatonin signal and reproductive response to photoperiod (reviewed in Turek and Van Cauter, 1994).

It is known that melatonin binding sites are present in various regions of the brain and peripheral tissues (Kokkola and Laitinen, 1998; reviewed in Morgan et al., 1994). In vitro autoradiography studies have used the biologically active agonist 2-[^125]Iiodomelatonin (IMEL) to show that in mammalian species studied to date, the SCN and the pars tuberalis (PT) of the anterior pituitary consistently bind to IMEL at levels above the detection limit of the method, while distribution in other brain areas is more variable across species (reviewed in Morgan et al., 1994). The PT is the only brain region containing melatonin binding sites in all seasonally breeding animals studied to date and is a potential site for melatonin’s action on the reproductive system (Morgan et al., 1994). However, in vitro autoradiography with IMEL will not detect low levels of melatonin
receptors. Therefore, the lack of IMEL binding in does not necessarily mean that melatonin receptors are lacking in a given brain region.

Recently, a number of molecular studies have resulted in the cloning and characterization of three subtypes of G-protein coupled melatonin receptors in vertebrates, designated Mel_{1a}, Mel_{1b}, and Mel_{1c} (reviewed in Kokkola and Laitinen, 1998). At present, only the Mel_{1a} and Mel_{1b} receptors are known to be present in mammals (Reppert, 1997). In situ hybridization analysis has determined that Mel_{1a} mRNA transcripts are expressed in the SCN and PT, areas that also exhibit IMEL binding (Reppert et al., 1994, 1995a, 1995b; Roca et al., 1996; Gauer et al., 1998; Weaver et al., 1996). Distribution of Mel_{1a} mRNA and melatonin binding sites within these brain regions has led to the hypothesis that the Mel_{1a} and Mel_{1b} receptors may mediate the circadian and reproductive effects of melatonin. However, more recent evidence has shown that the Mel_{1a} receptor may solely account for melatonin’s effects on reproduction and circadian timing (Weaver et al., 1996; Liu et al., 1997).

In vitro autoradiography and melatonin receptor cloning studies have allowed an examination of receptor gene expression in brain areas that regulate circadian rhythms and reproduction. In seasonally breeding mammals, the location and mechanism of melatonin’s action on the reproductive system is uncertain. Potential sites for the reproductive effects of melatonin as determined by in vitro autoradiography analysis include the PT, SCN, medial preoptic area (MPOA), anterior hypothalamus (AH), mediobasal hypothalamus (MBH), and the bed nucleus of the stria terminalis (BNST) (Glass and Lynch, 1981; Lincoln and Tortonese, 1995; Malpaux et al., 1998; Maywood et al., 1996; Maywood and Hastings, 1995; Morgan et al., 1994; Morgan et al., 1996;
Ratiere et al., 1997; Heideman et al., 1999a). An attractive hypothesis is that melatonin somehow interacts with GnRH neurons of brain areas that also show melatonin binding sites. However, it is yet to be shown that melatonin receptor mRNA is expressed in GnRH neurons in the hypothalamic regions. Recently, Song et al. (1998) presented data that showed colocalization of melatonin-la mRNA transcripts in vasopressin containing neurons of the hamster SCN, implicating this site as a potential target for melatonin’s circadian or reproductive effects. Vasopressin neurons of the SCN act to modulate neuronal firing rate in the SCN itself and also mediate circadian outputs to other hypothalamic areas, such as the paraventricular nucleus (PVN) and anteroventral hypothalamus (AVH) (Jin et al., 1999).

Phenotypic variation in photoresponsiveness

It is clear that in reproductively photoresponsive mammals, information concerning daylength is transduced through the complex neuroendocrine pathway described above and integrated by the central nervous system, resulting in photoperiodic regulation of reproductive state. However, not all mammals respond equally to seasonal changes in photoperiod. Variation in the ability to use daylength as a regulator of reproduction exists between species, between geographically isolated populations of the same species, and between individuals within the same population (reviewed in Bronson and Heideman, 1994). Outbred laboratory colonies derived from wild-caught deer mice (Peromyscus maniculatus; Blank and Dejardins, 1986; Dejardins and Lopez, 1983; Dejardins et al., 1986), white-footed mice (Peromyscus leucopus; Heideman and Bronson, 1991; Heideman et al., 1999b; Lynch et al., 1981), Djungarian hamsters
(Phodopus sungorus; Lynch et al., 1989; Puchalski and Lynch, 1986), meadow voles (Microtus pennsylvanicus; Dark and Zucker, 1984; Kerbeshian et al., 1994), prairie voles (Microtus ochrogaster; Nelson, 1985) and field voles (Microtus agrestis; Spears and Clarke, 1988) contain both reproductively photoresponsive and nonresponsive individuals. Selection experiments have significantly altered the proportion of photoresponsive individuals within laboratory populations of deer mice (Dejardins et al., 1986), white-footed mice (Heideman and Bronson, 1991; Heideman et al., 1999b), Djungarian hamsters (Lynch et al., 1989; Kliman and Lynch, 1992), and field voles (Spears and Clarke, 1988) and demonstrated that variation in photoresponsiveness has a genetic basis.

The mechanisms that determine phenotypic variation in reproductive photoresponsiveness in most mammalian species are not fully understood. It is possible that modifications at one or several levels in the neuroendocrine pathway transducing photoperiodic information to the hypothalamic-pituitary-gonadal (HPG) axis may account for variation in photoresponsiveness among rodents. First, circadian system variation between photoresponsive and nonresponsive individuals may result in differential measurement of photoperiodic time. Second, a change in the short day melatonin signal or sensitivity to melatonin may result in nonresponsiveness. Third, differences in the melatonin effector pathway, such as melatonin receptor distribution and receptor coupling to cellular signal transduction pathways. Finally, differences in GnRH neuron abundance or secretion may exist between photoresponsive and nonresponsive individuals.
Significance

In no species do we fully understand natural variation in the genetics and physiology of normal (i.e. non-pathological) brain function. Understanding genetic variation in the neural pathways that control physiological function is both necessary and important for progression in biomedical research and the treatment of disease. In addition, the study of natural variation will help determine the relationship between normal brain variation and brain function and the evolution of brain pathways. The effectiveness of drug medications for the treatment of a given condition may depend wholly on individual variation in the brain pathway targeted by the medication. The study of natural variation in brain function may reveal potential areas in a neural pathway that cause differences in individuals of a given species. The discovery of natural variation will most certainly benefit medical research in determining if differential effects of a particular medical treatment may be due in part to differences in brain function between individuals.

Studies concerned with physiological questions almost always use highly inbred laboratory animal populations such as the laboratory rat (*Rattus norvegicus*), the laboratory mouse (*Mus musculus*), the Syrian hamster (*Mesocricetus auratus*), and the Djungarian hamster (*Phodopus sungorus*) (Blank, 1992, and references therein). These animal models typically exhibit clear physiological responses to experimental manipulation because much of the intra-individual genetic variation has been removed through generations of selective inbreeding. Inbred lines often exhibit a uniformity of physiological function that is important (and sometimes necessary) towards elucidating neural pathways involved in a particular physiological response to the environment. In
natural populations, however, individuals differ in type and extent of many physiological traits (Blank, 1992). Therefore, inbred laboratory populations do not display genetic variation in brain function seen in natural populations.

The white-footed mouse (*P. leucopus*) is an attractive animal model to study natural variation in brain function. It is a small cricetine rodent found across North and Central America, easily trapped and bred in captivity. Outbred populations of white-footed mice derived from wild-caught individuals represent the genetic variation in brain function seen in natural populations much more accurately than the typical inbred laboratory strain used in physiological research. Natural populations of white-footed mice are known to be highly genetically variable in reproductive photoresponsiveness. Thus, the white-footed mouse provides an outbred, wild animal model that likely contains evolutionarily-important genetic and phenotypic variation in photoresponsiveness relevant to natural populations.

Intraspecific comparisons of photoperiodic responsive and nonresponsive mice provide an opportunity to study the evolution of alternative reproductive strategies within a single species. Comparing differences in physiological, cellular, and molecular mechanisms involved in the neuroendocrine pathway regulating photoresponsiveness will ultimately reveal the gene(s) acted upon by evolution to produce variation in seasonal reproductive strategies. In addition, understanding the mechanisms that result in individual variation in photoresponsiveness is directly applicable to the treatment of certain human medical disorders, such as circadian-based sleep disorders, seasonal affective disorder, and jet-lag (Srinivasan 1997; Wehr, 1997; Zisapel, 1999).
CHAPTER TWO

Circadian Rhythms and Photoresponsiveness in the White-footed mouse, 

*Peromyscus leucopus*

Introduction

Individual variation in reproductive photoresponsiveness is well documented in *Peromyscus leucopus* (Heideman and Bronson, 1991; Heideman et al., 1999b; Lynch et al., 1981). Although the mechanism(s) causing variation in photoresponsiveness in this species is not known, several hypotheses have been presented to explain the phenomenon. Potentially, individual variation in photoresponsiveness could result from at least (1) variation in transduction of light information via the retinohypothalamic tract (RHT) to the circadian system, the suprachiasmatic nuclei (SCN) of the hypothalamus; (2) an alteration in circadian function, resulting in differences in photoperiodic time measurement; (3) differences in melatonin production in short days; (4) differences in melatonin receptor abundance and/or distribution; and (5) changes in the melatonin effector pathway responsible for transducing the melatonin signal to the hypothalamic-pituitary-gonadal axis.

Researchers have determined that the length of nocturnal secretion of melatonin controls reproductive state in seasonally breeding rodents (Dowell and Lynch, 1987; Blank and Freeman, 1991; Carter and Goldman, 1983). Nonresponsive individuals of several species can vary in their response to short day melatonin signals administered exogenously (Blank and Freeman, 1991; Carlson et al., 1989; Heath and Lynch, 1982; Margraf and Lynch, 1993; Stirland et al., 1996b). For example, nonresponsive
Djungarian hamsters produce a long day melatonin signal during short day photoperiods (Puchalski and Lynch, 1986). In *P. maniculatus* and *P. leucopus*, nonresponsive individuals can distinguish long and short days, as they exhibit the typical long-duration nocturnal melatonin pulse also seen in photoresponsive mice under short day photoperiods (Blank and Nelson, 1988; Heath and Lynch, 1982). In addition, pinealectomized nonresponsive mice are insensitive to the reproductive effects of melatonin administered by injection or subcutaneous implantation (Blank and Freeman, 1991; Carlson et al., 1989; Heath and Lynch, 1982).

The latter studies imply that variation in the melatonin effector pathway may be a mechanism for nonresponsiveness in *P. leucopus*. Weaver et al. (1990) showed that nonresponsive mice from Georgia and photoresponsive *P. leucopus* from Connecticut exhibited similar binding patterns of $^{125}$I-labeled melatonin (IMEL) in brain sites known to express melatonin receptors. In addition, melatonin inhibited forskolin-stimulated cAMP accumulation in pars tuberalis (PT) explants occurred from both populations, suggesting that there are no differences in melatonin receptor-effector coupling between photoresponsive and nonresponsive mice (Weaver et al., 1990). Conversely, Heideman et al. (1999a) recently demonstrated a greater number of melatonin binding sites in nonresponsive *P. leucopus* within the medial preoptic area (MPOA) and bed nucleus of the stria terminalis (BNST).

Other studies have demonstrated that variation in the circadian system can influence photoperiodism in rodents. Nonresponsive Djungarian and Syrian hamsters from laboratory populations exhibit altered circadian characteristics such as free-running period (tau) in constant darkness, splitting patterns in constant light, differences in phase
response curves (PRC) to brief pulses of light, duration of activity (alpha) in short
photoperiods, and phase angle of entrainment (Loudon et al., 1998; Puchalski and Lynch,
1986, 1988, 1991, 1994; Ralph and Menaker, 1988; Shimomura et al., 1997; Stanfield
and Horton, 1996; Stirland et al., 1996a, 1996b). Several experiments have demonstrated
that nonresponsive hamsters are unable to measure photoperiodic time in a 24 hour day,
but can be made to exhibit photoperiodism under specific light cycles that approximate
the length of their free-running periods (Puchalski and Lynch, 1994; Loudon et al., 1998;
Shimomura et al., 1997).

It is unclear if circadian system variation accounts in part for variation in
photoresponsiveness in *P. leucopus*. Evidence gathered from resonance and T-cycle
studies has demonstrated that the circadian system is involved in photoperiodic time
measurement and reproductive development in *P. leucopus* (Sullivan and Lynch, 1986).
Carlson et al. (1989) reported no differences in free-running period, duration of activity in
short or long days, or phase angle of activity in short or long days, between juvenile mice
from a nonresponsive population of Georgia *P. leucopus* and a population of Connecticut
mice that was largely photoresponsive. However, the investigators used small sample
sizes (7 vs. 4) and did not test responsiveness to short day photoperiod before measuring
activity rhythms. In addition, Johnston and Zucker (1980) found no relationship between
phase angle of activity in short days and testicular index (length x width) from a
population of Michigan mice.

The purpose of this study was twofold: (1) to test the hypothesis that variation in
the circadian system can alter photoresponsiveness within our population of *P. leucopus*;
and (2) to compare results of this study, done on a single, outbred population of Virginia
mice, with the results of Carlson et al. (1989), who investigated circadian attributes of geographically separated populations of juvenile *P. leucopus*. Circadian control of melatonin production and photoresponsiveness in other seasonal species indicates that this system may be a source of variation that can determine the reproductive capacity of *P. leucopus* during the winter months. I predicted that circadian variation would not be the mechanism for individual variation in photoresponsiveness within an outbred population of *P. leucopus* for two reasons: (1) circadian variation could potentially impact the regulation of many physiological and behavioral processes necessary for survival in natural populations; and (2) Carlson et al. (1989) found, despite small sample sizes, no differences in circadian attributes between populations of photoresponsive and nonresponsive juveniles. Therefore, experiments in this study were designed with larger sample sizes to allow for strong conclusions from negative data. My data suggests that some subtle differences in circadian activity patterns do exist between responsive and nonresponsive white-footed mice from a single, recently-derived, outbred Virginia population. However, it appears that these differences are not biologically important to the regulation of reproduction in *P. leucopus*.

**Methods**

**General Animal Care and Maintenance**

*P. leucopus* used in this study were fourth and fifth generation offspring from an outbred laboratory population originally trapped near the College of William and Mary in Williamsburg, VA (Heideman et al., 1999b). Newborn animals were transferred within 2 days of birth from a long day length (L16:D8; lights on at 4:00 am EST; LD) to a short
day length (L8:D16; lights on at 8:00 am EST; SD), weaned at 22 +/- 1 days of age, and
caged individually in polyethylene cages (27 x 16 x 13 cm) with wire tops, 3 cm pine
shavings, and ad libidum access to food (RMH 2000, Southern States Cooperative,
Williamsburg, VA) and tap water. Animal rooms were maintained at 23 +/- 2°C with an
illuminance that varied from 200-800 lux for experiment 1 and 2, and 120-800 lux for
experiment 3.

DETERMINATION OF REPRODUCTIVE PHENOTYPE

At 70 +/- 3 days of age, animals were transferred to a separate building for
identification of reproductive phenotype. Male mice were lightly anesthetized with
methoxyflourane (Pitman-Moore Inc., Mundelein, IL), and length and width of the right
testis was measured through the scrotum with calipers. Testis length was multiplied by
width to obtain a testis index. Females were maintained at a deep surgical level of
anesthesia with methoxyflourane, and reproductive organs were examined through a
small lateral incision into the abdominal cavity. Females received a reproductive index
score ranging from 1 (tiny ovaries, usually <2 mm in greatest length, lacking visible
follicles or corpora lutea, and a uterine diameter ≤ 0.5 mm) to 5 (large ovaries, usually
>3.5 mm in greatest length, with large follicles or corpora lutea and a uterine diameter
>1.0 mm). A rank of 3 was given to females exhibiting an intermediate phenotype
(ovaries usually 2.5-3.5 mm, small follicles or corpora lutea, and uterine diameter
between 0.5-1.0 mm), while scores of 2 or 4 represented females not fully meeting the
criteria for the extreme categories (Heideman et al., 1999b). Measurements were taken
by an individual (PDH or TAB) blind with respect to treatment. Surgical incisions were
closed with stainless steel wound clips (MikRon Precision Inc., Gardena CA) that were removed 3-4 days after surgery. Mice were ear-tagged (Size 1 Monel; National Band and Tag Co., Newport, KY) and weighed after assessment of reproductive phenotype and returned to cages for recovery.

Animals were classified as photoresponsive, intermediate, or nonresponsive according to reproductive index scores. Males with a testis index <24 mm$^2$ and females with a rank of 1 or 2 were classified as photoresponsive, while males with a testis index >32 mm$^2$ and females with a rank of 4 or 5 were classified as nonresponsive. Intermediate mice consisted of males with a testis index >24 mm$^2$ but <32 mm$^2$ and females with a score of 3 (Heideman and Bronson, 1991). Breeding lines of photoresponsive and nonresponsive mice were generated by selection using these criteria (Heideman et al., 1999b). An unselected control line was also generated and examined for circadian characters.

**Experiment 1: Measurement of Circadian Rhythms**

In order to test the hypothesis that differential organization of the circadian system in *P. leucopus* may alter an animal's ability to respond to photoperiod, running wheel activity was recorded during five trials (from March 1998-April 1999 and September-October 1999) for 16 photoresponsive males, 17 photoresponsive females, 18 nonresponsive males, and 16 nonresponsive females, ages 70-90 days. Only photoresponsive offspring from the photoresponsive line and nonresponsive offspring from the nonresponsive line were used in this experiment.
Animals were individually housed in large polyethylene cages (45 x 23.5 x 20.5 cm) equipped with running wheels, 1-2 cm pine shavings, and ad libidum access to food (Harlan Teklab, Madison, WI) and tap water. Cages were placed in a Revco Environmental Chamber (Revco, Asheville, NC) that maintained a temperature of 23 +/- 1°C. Total number of wheel revolutions were recorded in 6-minute bins, plotted as activity records, and analyzed using software developed by Dr. Roberto Refinetti (@www.personalconsulting.com).

Mice were subjected to the following photoperiod schedule, modified from Carlson et al. (1989): 9-10 days short day (L8:D16; lights on at 8:00 am EST; SD), 26 days long day (L16:D8; lights on at 4:00 am EST; LD), and 14 days in constant dark (DD). LD was extended from this protocol during one trial (Nov. 1998- Jan. 1999) because a severe ice storm caused power surges at the College of William and Mary for approximately 10 days, disrupting data collection and the LD light cycle several times.

In short days, but not long days or constant dark, our population of *P. leucopus* showed a considerable degree of variation in activity onset patterns. Some mice began running shortly after lights off and continued a steady pattern of activity throughout most of the dark period (for example see figure 2a, mouse #2011). Others showed a splitting pattern of activity at the beginning of the dark period: a brief burst of activity at or near lights off was followed by a steady pattern of activity approximately 1-3 hours later (Figure 2b, mice #2017 and 2013). Conversely, mice showed little or no variation in activity onset patterns in long daylengths and constant darkness (see Figures 2a and 2b).

In addition, some mice exhibited clear activity patterns but ran fewer revolutions during their active cycle. Records for these mice revealed a pattern that consisted of
many small bursts of activity throughout the dark period (see mouse #2018, Figure 2a). This pattern was in clear contrast to the majority of mice that ran steadily, with few breaks, throughout the dark period (Figures 2a and 2b).

In light of the variation seen in activity onset during short days, it was necessary to test different methods of activity measurement to determine the most accurate means of estimating onset. I tested three sets of rules to define activity onset: (1) onset defined as the beginning of the period of activity that lasted 24-30 minutes, is preceded by at least 2 hours of no sustained activity, and is not separated by subsequent activity for more than 1.5 hours (adapted from Darrow and Goldman, 1985; Puchalski and Lynch, 1994; Stanfield and Horton, 1996); (2) an eye-fitted line drawn, while blind to treatment, through onset and offset for consecutive days, and the time in hours between the lines determined (Carlson et al., 1989; Puchalski and Lynch, 1988, 1991; Margraf and Lynch, 1993; Kliman and Lynch, 1991; Sullivan and Lynch, 1986; Millette and Turek, 1986); and (3) onset defined as the first bout of activity that lasted at least two recording bins (12 minutes) and was preceded by at least two hours of zero sustained activity. In all three cases, activity offset was defined as the end of the last bout of activity that occurred before a 2-hour period with no sustained activity (less than 4 bins, or 24 minutes, of total activity).

Analysis of data from 20 mice in long days and 64 mice in short days produced mean durations of locomotor activity that were statistically similar among all rules compared. Rules (2) and (3) produced means that were nearly identical to each other. Rule set (1) tended to exclude activity during the very beginning of the dark period and resulted in lower values of alpha for mice in short days. Duration of activity in DD was
not compared in this manner because visual inspection of the data from 86 mice revealed a consistent pattern of activity onset that would have caused little or no variation in activity estimates under each rule set.

Since all methods compared produced similar qualitative results, rule set (3) was chosen over the more commonly used eye-fitted line approach because it offered ease of measurement with our activity data collection software. In addition, a separate method of analysis was used to calculate activity duration for mice that ran in sporadic bursts throughout the dark period. For these mice, activity onset was defined to have begun when activity first increased by 50% over a 1-hour time span. Activity offset had occurred when mice decreased their activity by 50% over a 1-hour time span.

Alpha (α), the duration of locomotor activity, was determined by calculating the time (in hours) between activity onset and offset for the last 5-6 days of SD and the last 7-10 days of LD and DD. Tau (τ), the free-running period, was determined by estimating the time (in hours) between successive activity onsets during the last 7-10 days of DD. Phase angle, the difference in hours between activity onset and lights off, was calculated for the last 5-6 days of SD and the last 7-10 days of LD. Data from consecutive days were averaged to determine values for α, τ, and phase angle. Days that did not exhibit a clear activity onset or offset were not used in the estimation of circadian parameters. Excluded data were replaced, if possible, by data from the nearest day(s) that bordered the sampling period described above. Mice were excluded from analysis for a particular photoperiod treatment if they did not exhibit at least five days of clear activity onset and offset patterns. Mice were completely excluded from analysis if they showed no signs of stable running or entrainment patterns under any of the photoperiod treatments.
Activity patterns were recorded during fewer consecutive days under the short photoperiod than the long photoperiod and constant darkness (10, 26 and 14 days, respectively). As a result, the sampling period defined for short daylengths was shorter than the sampling period for long daylengths and constant darkness. Because mice exhibit several days of transient patterns of activity as they entrain to new photoperiods (Pittendrigh and Daan, 1976), data from the first two days of short day, the first five days of long day, or the first four days of DD photoperiods were not used. Animals entered the experimental short daylengths already entrained to this photoperiod. Therefore, only the first two days of short day photoperiod were excluded from analysis in order to control for possible effects of running wheel acclimation on activity patterns.

**Experiment 2: Correlation between Circadian Characters and Pubertal State**

Seventeen control line males with access to running wheels were exposed to the photoperiod schedule described above from September-October 1998 to determine if there was a correlation between circadian characters and pubertal state, as measured by the extent of testicular development and body weight. No control line females were used because of the difficulty in accurately determining the exact time of puberty. Data analysis was performed as described above. For each animal, testis indices were recorded at 70 ± 3 days of age (before exposure to experimental regime).

**Experiment 3: Constant Darkness (DD) Assay of Photoresponsiveness**

This experiment tests the hypothesis that variation in photoresponsiveness within our *P. leucopus* population may result from differential measurement of photoperiodic
time due to differences in the circadian system of photoresponsive and nonresponsive mice. This hypothesis was tested by exposing young mice from the responsive and nonresponsive lines to constant darkness from 23 ± 2 days of age to 70 ± 3 days of age. If nonresponsive mice undergo gonadal development because light illuminates the photosensitive phase of their circadian rhythm of photoperiodic photosensitivity (CRPP) even during short days, then these mice should exhibit gonadal regression if the photostimulatory signal is completely removed during exposure to constant darkness. The null hypothesis, on the other hand, states that nonresponsiveness in *P. leucopus* results from non-circadian system differences in the neuroendocrine pathway that regulates seasonal reproduction. If nonresponsive mice exhibit gonadal growth in constant darkness, then these mice may exhibit neuroendocrine differences somewhere independent of the SCN, such as melatonin receptor distribution and cellular signal transduction, resulting in the nonresponsive phenotype.

From February through August 1999, Male and female *P. leucopus* were weaned at 23 +/- 1d of age, individually housed in small cages described above, and transported within 5 days of weaning from the population laboratory to photoperiod boxes located in Millington Hall. The boxes could house 8 or 21 small animal cages. Twelve males and females from the nonresponsive and photoresponsive lines were subjected to constant darkness (DD) or short day (L8:D16; lights on at 8:00 am EST; SD) photoperiod until 70 +/- 3 days of age.

Mice were then euthanized by CO₂ inhalation, weighed and autopsied to check gonadal development. Mice received a small incision across the ventral abdominal wall
and were opened by blunt dissection. Testes and seminal vesicles or ovaries and uteri were removed from male and female mice, respectively, and weighed while still wet.

One responsive male in DD was removed from analysis as a statistical outlier because of its unusually large seminal vesicles (144.4 mg; 10.88 standard deviations away from the paired seminal vesicle mean for responsive males in DD). Inclusion or removal of this animal had no effect on statistical comparisons for body weight, paired testes weights, or paired seminal vesicle weights. Although this measure falls within the expected range of seminal vesicle weights for *P. leucopus* (Eric Bradley, personal communication), it was by far the largest measure encountered in the entire study.

**Statistical Analysis**

Means and standard errors of the means are presented for gonadal measurements, body weights, and circadian parameters (\(\alpha, \tau\), phase angle). Circadian parameters were compared between selected lines and between sexes using 2-way factorial ANOVA (Statview, Power Macintosh and SPSS Version 8.0 for Windows; \(p < 0.05\) level of significance). Effects of photoperiod treatment and lineage on gonadal development were also tested by a 2-way factorial ANOVA. The following planned post-hoc comparisons of gonadal development were analyzed by two-tailed unpaired t-tests (\(p < 0.05\) level of significance): (1) responsive vs. nonresponsive males or females in DD; (2) responsive or nonresponsive males or females in SD; (3) nonresponsive males or females in SD vs. DD. Results were graphed using SigmaPlot for Windows. A series of power analyses (\(P = 0.8, 0.05\) level of significance) were also performed post-hoc to determine how sensitive
our sample sizes were at detecting differences in circadian characters between selected lines.

Results

Experiment 1:

Nonresponsive mice displayed a significantly longer tau than responsive mice (p = 0.0083, 2W ANOVA), due primarily to the significantly longer tau of female nonresponsive mice compared to nonresponsive males (p = 0.0003, 2-tailed t-test; Table 1, Figure 3; need to update this post-hoc comparison). Male and female nonresponsive mice did not differ significantly from responsive males and females in measurements of short day α, short day phase angle of activity, long day α, or long day phase angle of activity (Table 1, Figures 4-5). Female mice showed a significantly larger long day phase angle of activity than male mice (p = 0.0424, 2W ANOVA), but there were no significant differences between nonresponsive and responsive mice (Table 1; Figure 5b). In other words, both responsive and nonresponsive female mice delayed the onset of nocturnal activity during long days to a greater degree than male mice of the same phenotypes. Sample sizes used in this experiment (n = 10 as a minimum) had sufficient power to detect differences in free-running period, short day phase angle of activity, short day duration of activity, long day phase angle of activity, and long day duration of activity that might be expected to be biologically relevant to the regulation of reproduction (Table 4).
**Experiment 2:**

Variation in tau, alpha, and phase angle of activity occurred within each selected line as well as between selected lines. To determine if a relationship between these circadian parameters and the extent of photoresponsiveness existed, testis index (TI = length x width) and body weight (BW) were measured from male mice from the unselected control line. There was no significant relationship between any of the circadian parameters (tau, short day alpha, short day phase angle, long day alpha, long day phase angle) and the extent of photoresponsiveness indicated by testis index or body weight (Figure 6; Table 3).

**Experiment 3:**

I predicted that responsive and nonresponsive mice would exhibit similar levels of gonadal development in constant dark if circadian differences were responsible for producing variation in reproductive state. However, I found that nonresponsive males developed large testes even in DD, while the responsive controls were reproductively inhibited to the same extent as expected in DD and SD. Across photoperiodic treatments (SD and DD), nonresponsive males exhibited larger paired testis weights (PTW) and larger paired seminal vesicle weights (PSVW) than photoresponsive males at 70 ± 3 days of age (2W ANOVA, PTW: p = 0.0001; PSVW: p = 0.0001; Figure 7). There was no significant effect of photoperiod treatment or interaction effect for either parameter measured. Planned post-hoc comparisons (t-tests) revealed statistically significant differences in paired testes weights and paired seminal vesicle weights between responsive and nonresponsive males exposed to DD and SD (Figure 7). Nonresponsive
males also exhibited greater body weights than responsive males (2W ANOVA, BW: p = 0.008), but post-hoc comparisons revealed significant differences in body weight only between nonresponsive and responsive males exposed to DD (Figure 9).

Differences in gonadal state were also evident between nonresponsive and responsive females exposed to constant darkness and short days. Nonresponsive females exhibited a greater mean paired ovarian weight (POW) and uterine weight (UW) than responsive females across photoperiodic treatments (SD and DD; 2W ANOVA, POW: p = 0.001; UW: p = 0.0006). However, post-hoc comparisons showed statistically significant differences in paired ovary weights and uterine weights between nonresponsive and responsive females exposed to DD but not SD (Figure 8). In addition, nonresponsive females exhibited greater body weights than responsive females exposed to both DD and SD (2W ANOVA, BW: p = 0.0043; Figure 9).

It was predicted that if circadian differences are responsible for variation in reproductive state, then nonresponsive mice in constant darkness would exhibit less gonadal development in constant darkness than in short days. Contrary to this prediction, gonadal development was qualitatively similar for nonresponsive mice in constant darkness or short days. Nonresponsive males in constant dark and short day photoperiods exhibited similar paired testes weights and paired seminal vesicle weights (Figure 7). Likewise, nonresponsive females in constant dark and short day photoperiods exhibited similar paired ovary weights and uterine weights (Figure 8).
Discussion

*Circadian differences and photoresponsiveness in Peromyscus leucopus*

Female nonresponsive mice exhibited significantly longer free-running periods in constant darkness than photoresponsive females (24.26 h vs. 23.74 h, respectively). This difference caused nonresponsive mice, as a group (males and females), to exhibit a significantly larger free-running period than responsive mice (24.08 h vs. 23.75 h). A sex difference in phase angle of locomotor activity in long days also occurred: females, as a group, phase delayed the onset of nocturnal activity to a greater degree than males. However, no differences in phase angle of activity under short or long days, or duration of activity under short or long days, were found between photoresponsive and nonresponsive mice.

Differences in circadian characters of locomotor activity in our population of white-footed mice do not appear to be biologically relevant to photoperiodic regulation of reproduction. First, there was no correlation between pubertal development and any of the circadian characters measured in the unselected control line males. Second, if the circadian system in nonresponsive mice causes them to interpret daylength differently, then it would be expected that juvenile nonresponsive mice would undergo a delay in gonadal development in conditions of constant darkness. However, there was no evidence for pubertal delay in nonresponsive mice: juvenile male and female nonresponsive mice exhibited significantly larger testes and seminal vesicle or ovary and uterine weights, respectively, than their photoresponsive equivalents in both short day and constant dark. Furthermore, gonadal state of nonresponsive mice was qualitatively similar in constant darkness and short daylengths. In addition, photoresponsive mice in
constant darkness and short daylengths did not differ in reproductive state. These results indicate that despite some statistically significant differences in circadian activity patterns, photoresponsive and nonresponsive mice measure photoperiodic time in a similar manner.

**Comparisons with studies on inbred laboratory populations**

My results contrast sharply with previous studies of the circadian system and photoresponsiveness in inbred laboratory populations. Variation in the circadian system has resulted in reproductive nonresponsiveness in at least two species of inbred laboratory rodents. The Djungarian hamster, *Phodopus sungorus*, has photoresponsive and nonresponsive individuals within laboratory populations (Puchalski and Lynch, 1986). Nonresponsive individuals have longer free-running periods in constant darkness, exhibit a pronounced phase delay in the onset of nocturnal activity under short days, shorter duration of activity in short days, and fewer instances of ‘split’ activity rhythms in constant light (Puchalski and Lynch, 1986, 1988). The phase delay in short day activity rhythms resembles a remarkably similar phase delay in melatonin secretion in the same photoperiod (Puchalski and Lynch, 1986). Although our nonresponsive mice exhibited longer free running rhythms, they completely lacked the phase delay in activity onset and the decrease in nocturnal activity during short days associated with an abnormal short day melatonin rhythm. My results demonstrate that nonresponsive mice tended to phase advance activity slightly in short days relative to responsive mice (Table 1). A post-hoc power analysis (Table 4) demonstrated that sample sizes used in this study (n = 10 per treatment group) were large enough to detect differences in phase angle and duration of
activity during short days that might be expected to occur if circadian system variation was the major cause of nonresponsiveness in *P. leucopus*.

In addition, nonresponsive Djungarian hamsters can be made to exhibit gonadal regression under specific T-cycles that approximate the length of their longer free-running periods (Puchalski and Lynch, 1994). Nonresponsive hamsters can also exhibit gonadal regression when given short day melatonin infusions during short day photoperiods (Puchalski et al., 1988). These experiments demonstrate that differences in aspects of photoperiodic time measurement controlled by the circadian system resulted in a long day melatonin rhythm in nonresponsive Djungarian hamsters, rendering them incapable of reproductive inhibition.

The single, semi-dominant *tau* mutation in the Syrian hamster, *M. auratus*, accelerates the free-running period of activity from 24 h in the wild-type to 20 h in the homozygous mutant (Ralph and Menaker, 1988). *Tau* mutants hamsters do not exhibit gonadal regression typical of the wild-type under short daylengths unless the period (T) of the photocycle is manipulated to equal the mutant free-running period of 20 hours (Stirland et al., 1996a; Shimomura et al., 1997). In addition, both *tau* mutants and wild-type individuals exhibit gonadal regression under constant darkness (Stirland et al., 1996b). Clearly, nonresponsiveness in *tau* mutants results from a circadian error in measuring photoperiodic time during 24 hour cycles seen in natural conditions.

*Comparisons with studies on other outbred populations*

In contrast to results from inbred laboratory populations of rodents, the few previous studies concerning variation in photoresponsiveness in outbred *P. leucopus*
colonies suggest that intraspecific differences in photoresponsiveness between populations are not due to circadian differences. If variation in the circadian system causes reproductive nonresponsiveness in *P. leucopus*, the following would be expected to occur (based on results from studies of inbred populations): (1) nonresponsive mice would exhibit differences in circadian characters, such as free-running period, phase angle of activity, and duration of activity, under various light cycles; (2) melatonin secretion, directly controlled by circadian system via the SCN, would be altered during short day exposure in nonresponsive individuals; and (3) gonadal regression could be induced in nonresponsive individuals by administration of short-day melatonin levels.

No evidence has been found in past studies to support any of these predictions. Carlson et al. (1989) demonstrated that nonresponsive mice from a Georgia population did not differ from Connecticut mice derived from a largely photoresponsive population in free-running period, phase angle of activity in long and short days, or duration of activity in long day, short day, or constant darkness. These populations did exhibit differences in their sensitivity to melatonin: Connecticut mice respond to exogenous administration of melatonin with gonadal involution, while Georgia mice are completely insensitive to the reproductive effects of melatonin (Carlson et al., 1989; Heath and Lynch, 1982). In addition, both Georgia and Connecticut mice exhibit the same daily rhythm of melatonin production (Lynch et al., 1982).

Studies of intra-individual variation within a single population of the closely related deer mouse (*P. maniculatus*) present indirect evidence that circadian variation may be unimportant for the photoperiodic regulation of reproduction within a single, outbred, genetically-variable population. (Blank et al., 1988; Blank and Freeman, 1991).
Artificially selected lines of photoresponsive and nonresponsive deer mice exhibited similar pineal melatonin contents (Blank et al., 1988) and similar nocturnal rhythms of 6-sulphoxymelatonin (Ruf et al., 1997), the primary urinary metabolite of melatonin, during short day exposure. Furthermore, exogenous administration of melatonin caused gonadal regression in photoresponsive but not nonresponsive mice exposed to long days (Blank and Freeman, 1991).

This report is the first evidence that differences in free-running circadian rhythms do exist between photoresponsive and nonresponsive individuals within a single, highly-genetically variable population of *P. leucopus*. It has been suggested that in Syrian hamsters, a change in free-running period of approximately 0.5 h (30 minutes) could potentially alter the timing of seasonal reproduction or abolish seasonality entirely (Elliott and Goldman, 1981). Notably, responsive and nonresponsive female mice from this study differed in their free-running periods by approximately 0.5 h (0.48 h). However, in this population, differences in free-running period did not account for differences in reproductive capacity seen between responsive and nonresponsive mice. Even within the control line, individual variation in free-running period was not correlated with changes in reproductive state during short days (Table 2).

*Predictions about the basis of variation in photoresponsiveness*

Considering evolutionary pressures, it is not surprising that circadian differences do not account for control of seasonal reproduction in our recently-derived, outbred population of white-footed mice. Wild animals rely on the normal functioning of their circadian system for survival in natural conditions (Decoursey, 1997, 1998). In addition
to its effects on reproduction, the circadian system controls the timing of an amalgam of behaviors and physiological responses that cycle on a circadian and/or circannual basis.

Potentially, differences in circadian organization that cause changes in photoperiodic time measurement could also affect the timing of foraging, nest-building, pelage change, and other metabolic and behavioral adjustments important to the organism for its survival.

The importance of the circadian system in the wild has been demonstrated by DeCoursey (1998), who described the decreased survival of SCN-lesioned eastern chipmunks (*Tamias striatus*) in natural habitat compared to sham-lesioned and intact control animals. DeCoursey (1997) also described the alteration of diurnal foraging behaviors and survivorship in SCN-lesioned white-tailed antelope ground squirrels (*Ammospermophilus leucurus*) housed in a desert enclosure. She hypothesized that the circadian system is necessary to synchronize activity during times favorable for survival (Decoursey, 1997).

Because the circadian system is so important for survival and reproduction in the wild, I predict that phenotypic variation in photoresponsiveness is not caused by differences in circadian function in natural populations. The occurrence of circadian variation may be tolerated within inbred laboratory populations because of the absence of selective pressures. A possible result of inbreeding may be the occurrence and preservation of mutations that affect the circadian system and photoresponsiveness within populations of inbred laboratory stocks. Failure to eliminate such mutations from inbred laboratory populations may result from inadvertent selection for individuals that breed throughout the year, regardless of the light cycle. I propose that variation in photoresponsiveness in the wild is likely to result from changes in the genetics and
physiology of an organism that will not potentially alter other behaviors and processes important for survival.

*P. leucopus* is an appropriate animal model to describe natural variation in brain function as it pertains to photoperiodic regulation of reproduction. It is unlikely that the Syrian and Djungarian hamsters are suitable animal models for the study of variation in brain function that may occur in wild populations. Laboratory stocks of both species are highly inbred populations that have probably lost much of the genetic variation seen in natural populations through many generations of inbreeding (Blank, 1992). As a result, information gained from inbred stocks may not be testable in wild conspecifics. However, our population of white-footed mice is recently derived from a wild-caught stock and probably reflects the genetic variation of mice found in natural conditions.

**Conclusion**

Differences in circadian attributes seen between photoresponsive and nonresponsive white-footed mice in this study are not relevant to the photoperiodic regulation of reproduction. This result, in conjunction with other published reports of endogenous melatonin rhythms and the effects of melatonin administration on reproduction in this species, lends support to the hypothesis that natural variation in reproductive photoresponsiveness is probably due to variation in the melatonin effector pathway (Lynch et al., 1989). Possible sources of variation at this level include melatonin receptor expression patterns and density, receptor coupling to cellular signal transduction pathways, and GnRH neuron density and regulation by synaptic inputs from various
regions of the brain. The next chapter will describe the partial molecular cloning of the melatonin-1a receptor in *P. leucopus*. 
CHAPTER THREE

Partial Molecular Cloning of the Melatonin-1a Receptor in the White-footed Mouse, *Peromyscus leucopus*

Introduction

Variation in the reproductive response to daylength occurs between species, between geographically isolated populations of the same species, and among individuals from the same population (reviewed in Bronson and Heideman, 1994). The neuroendocrine pathway controlling photoresponsiveness does so by regulating the nocturnal secretion of melatonin. The duration of melatonin secretion encodes an endocrine measure of daylength and determines the reproductive status of an individual responsive to photoperiod (reviewed in Chapter One).

Although the exact mechanism(s) for variation in photoresponsiveness remains unknown in many species, it has been hypothesized that differences in melatonin receptor abundance, distribution, or sensitivity may exist between photoresponsive and nonresponsive individuals (Heideman et al., 1999a; Weaver et al., 1990). Attempts to identify brain sites that contain melatonin receptors have involved the use of two techniques: (1) in vitro autoradiography with 2-[^125]Iiodomelatonin (IMEL), a biologically active analog of melatonin; and (2) gene expression studies using melatonin receptor cDNA clones. In vitro autoradiography has detected melatonin binding sites in the pars tuberalis (PT) of all seasonally breeding mammals studied to date (Morgan et al., 1994). Most mammals also show strong binding at the suprachiasmatic nuclei (SCN) of the hypothalamus (Morgan et al., 1994). Other brain regions that show binding are
variable across species and include the medial preoptic area (MPOA), anterior hypothalamus (AH), mediobasal hypothalamus (MBH), and the bed nucleus of the stria terminalis (BNST) (Glass and Lynch, 1981; Lincoln and Tortonese, 1995; Malpaux et al., 1998; Maywood et al., 1996; Maywood and Hastings, 1995; Morgan et al., 1994; Morgan et al., 1996; Ratiere et al., 1997; Heideman et al., 1999a).

Molecular cloning studies have demonstrated the existence of three types of melatonin receptors in vertebrates, designated the Mel\textsubscript{1a}, Mel\textsubscript{1b}, and Mel\textsubscript{1c} receptors (reviewed in Kokkola and Laitinen, 1998). Melatonin receptors belong to the G-protein coupled receptor (GPR) superfamily and share structural features with other GPRs (Morgan et al., 1994; Reppert, 1997). They consist of a single polypeptide chain with seven transmembrane domains connected by intra- and extracellular loops, an extracellular N-terminus, an intracellular C-terminus, and several amino acid residues conserved by all GPRs (Kokkola and Laitinen, 1998). However, several characteristics distinguish melatonin receptors from other GPRs: an NRY motif (instead of a DRY or ERY) just downstream from the third transmembrane domain, a C(C/Y)ICHS motif immediately downstream from NRY, and an NAXXY (rather than an NPXXY) motif in the seventh transmembrane domain (Reppert, 1997).

The Mel\textsubscript{1a} and Mel\textsubscript{1b} receptors are the only receptor subtypes found in mammals to date. Both receptors are coupled to a G-protein (G\textsubscript{i}) that is inhibitory to adenylyl cyclase and forskolin-stimulated cAMP production (Morgan et al., 1994; Reppert, 1997). The Mel\textsubscript{1a} receptor transcript is expressed in the mammalian PT and SCN, regions that also exhibit pronounced I-MEL binding (Gauer et al., 1998; Reppert, 1997; Reppert et al., 1994; Roca et al., 1996; Weaver et al., 1996). The full length cDNA for the Mel\textsubscript{1b}
receptor has been cloned only in humans, while fragments have been cloned in the laboratory rat (*Rattus norvegicus*), the laboratory mouse (*Mus musculus*), Djungarian and Siberian hamsters, chicken, zebrafish, and *Xenopus laevis* (Kokkola and Laitinen, 1998, and references therein; Reppert et al., 1995a, 1995b; Weaver et al., 1996). Human Mel₁ᵇ mRNA has been detected by RT-PCR in the retina, whole brain, and hippocampus, but not the SCN or PT (Reppert et al., 1995a).

Several lines of evidence indicate that the Mel₁ᵃ receptor subtype may mediate the circadian and reproductive effects of melatonin in some species (Kokkola and Laitinen, 1998; Reppert, 1997). First, the Mel₁ᵇ receptor does not appear to be expressed in human PT and SCN, areas important for regulation of reproduction and circadian rhythms, respectively (Reppert et al., 1995a). Second, in situ hybridization cannot detect Mel₁ᵇ transcripts in rat brain or pituitary (Reppert et al., 1995a). Third, two nonsense mutations present in the coding region of the Mel₁ᵇ receptor of Siberian hamsters (*Phodopus sungorus*) from laboratory populations causes expression of a truncated, non-functional receptor in this species (Weaver et al., 1996). Nonetheless, Siberian hamsters exhibit the following responses: (1) gonadal regression after exposure to short photoperiods; and (2) phase shifting of SCN electrical activity after application of melatonin in vitro. These results indicate that melatonin can regulate circadian rhythms and reproductive state despite a non-functional Mel₁ᵇ receptor (Weaver et al., 1996). In addition, mice bred with a targeted disruption of the Mel₁ᵃ receptor still exhibited phase shifts in response to melatonin treatment, demonstrating that the Mel₁ᵃ receptor is not solely responsible for melatonin’s circadian effects (Liu et al., 1997).
Very few studies have examined the hypothesis that intraspecific variation in reproductive photoresponsiveness is based on individual differences in melatonin receptor abundance, location, or affinity. Weaver et al. (1990) found no differences in the amount or location of IMEL binding between nonresponsive *P. leucopus* from a Georgia population and *P. leucopus* from a largely photoresponsive Connecticut population. However, their sample sizes (4 vs. 4) were too low to generate sufficient statistical power to support negative results. Also, it is possible that nonresponsive individuals from the Connecticut population were included in analysis, thereby obscuring differences between the populations (Heideman et al., 1999a).

Heideman et al. (1999a) tested the hypothesis that differences in melatonin binding might be a contributing factor in individual variation in photoresponsiveness within a single, highly variable population of *P. leucopus*. This population has individuals that are reproductively repressed and others that maintain mature reproductive status when exposed to short day photoperiods (Heideman et al., 1999b). Heideman et al. (1999a) found differences in IMEL binding in the medial preoptic area (MPOA) and bed nucleus of the stria terminalis (BNST) between selected lines of photoresponsive and nonresponsive individuals using a sample size (8 vs. 8) providing greater statistical power than Weaver et al. (1990). The higher statistical power generated in this study was necessary to detect the differences observed in IMEL binding (Heideman et al., 1999a).

The pattern of melatonin receptor gene expression in the white-footed mouse, *P. leucopus*, is unknown. It is also unknown if differences in melatonin receptor gene expression exist between reproductively photoresponsive and nonresponsive white-footed mice. This chapter reports the partial cloning of the Mel1a receptor from a *P. leucopus*
genomic library. Cloning of the *P. leucopus* Mel₁₄ receptor will allow an examination of receptor gene expression through in situ hybridization (ISH), RNase protection assays, and RT-PCR. Ultimately, these techniques may reveal if differences in brain expression patterns exist between photoresponsive and nonresponsive individuals. It is presently unknown if temporal and spatial patterns of melatonin receptor mRNA expression resemble patterns of melatonin binding sites as determined by in vitro autoradiography in *P. leucopus*. A major goal of this thesis is to produce a clone of the Mel₁₄ receptor that will be used to determine brain areas that express mRNA for the receptor. These results will be compared to studies that have used IMEL to reveal regions that contain melatonin binding sites.

The white-footed mouse is an appropriate model to study natural variation in brain function because laboratory populations are recently derived from wild-caught individuals and contain the genetic variability likely seen in wild populations. Studying Mel₁₄ receptor gene expression in the white-footed mouse is particularly attractive because it allows molecular analysis of an aspect of the neuroendocrine pathway controlling photoresponsiveness in a species that is highly genetically variable in their response to photoperiod. It is unclear whether molecular studies performed on inbred laboratory stocks, such as the laboratory rat (*Rattus norvegicus*), the laboratory mouse (*Mus musculus*), Syrian hamster (*Mesocricetus auratus*), and the Siberian hamster (*Phodopus sungorus*), will reveal variation in melatonin receptor gene expression contained in wild populations. It is necessary to use outbred populations such as laboratory stocks of white-footed mice to understand variation in the molecular genetics and physiology of brain function displayed in natural populations.
Methods

OVERVIEW

The following experiments were performed to clone the *P. leucopus* Mel₁₄ receptor. Mouse (*Mus musculus*) Mel₁₄ probes were used to screen a *P. leucopus* genomic library for homologous genes. The resulting clones were sequenced and subjected to BLAST searches in the GenBank database (National Library of Medicine) to determine if they were homologous to known melatonin receptor genes.

HOMOLOGY SCREENING APPROACH

All melatonin receptor genes isolated and sequenced to date contain two exons separated by a large (>8KB) intron (Reppert and Weaver, 1995). Two fragments of the mouse (*Mus musculus*) Mel₁₄ receptor were used as probes to screen for both exons in a *P. leucopus* genomic library. The first probe was a full length, 1.1 kb cDNA fragment of the entire coding region of the mouse Mel₁₄ receptor (generously provided to us by Steven Reppert, Laboratory of Developmental Chronobiology, Massachusetts General Hospital, Harvard University). Because the second exon contains the majority of the coding region of melatonin receptors (Kokkola and Laitinen, 1998), the full length mouse cDNA was used to screen for this exon. The first exon contains the first transmembrane region and the 5' untranslated region (5'UTR). A small (146 base pair) fragment encoding the first transmembrane region was excised from the 5' region of the full length mouse cDNA and used to screen the genomic library for the first exon.
**Homology screen for second exon of the Mel$_{1a}$ receptor**

The pcDNA-3 plasmid (1μl of 100ng/ml; Invitrogen) containing the 1.1 kb mouse Mel$_{1a}$ receptor cDNA fragment was transformed into DH5α competent cells. Briefly, 100 μl of transformation-competent DH5α cells were gently mixed with plasmid DNA, incubated on ice (30 minutes), heat shocked at 42°C (90 seconds), incubated on ice (5 minutes), and incubated at 37°C in Luria broth (LB) media for 1 hour. The mixture was spread evenly on LB plates containing 50 μg/ml ampicillin, 0.5 mg X-Gal, 0.8 mg IPTG and incubated for 6-8 hours at 37°C. Bacterial colonies were harvested and cultured overnight at 37°C in LB containing 50 ng/ml ampicillin.

Plasmid DNA was isolated by standard technique (modified from Sambrook et al., 1989) and digested with HindIII and XhoI restriction enzymes. The digested DNA was run on a 1.2% agarose gel and visualized with ethidium bromide. The 1.1 kb fragment visible on the gel was excised, purified according to manufacturer's protocol using the Gene-Clean Kit (Bio 101), and radiolabeled with α$^{32}$-dCTP (3000 Ci/mmol, New England Nuclear; 6.43 x 10$^6$ dpms) via a random priming reaction using the Prime-a-Gene kit (Promega).

An EMBL-3 *P. leucopus* genomic library (Peromyscus Genetic Stock Center, University of South Carolina) was plated with KW251 cells (Stratagene) on LB plates and incubated at 37°C for 8-12 hours, producing plaques (50,000 PFUs). Duplicates lifts were performed using nylon transfer membranes (Magnagraph Osmonics, Inc.). Phage was lysed by autoclaving (2 minutes at a pressure of 20 lbs./inch$^2$) and phage DNA was crosslinked to the filters by UV crosslinking (Fisher Scientific; optimum setting).
Filters were pre-hybridized in 30% formamide, 1M NaCl, 1% SDS, and 10 mM TRIS-HCl for 6 hours at 42 °C. Prehybridization buffer was removed and replaced with an identical buffer solution containing the radiolabeled mouse cDNA probe (8.65 x 10⁴ cpms/ml). Filters were incubated in hybridization solution overnight at 42 °C and washed with 2X SSC and 1% SDS for 10 minutes at room temperature for 10 minute intervals at 42 °C until decay measured from the filters by a GM counter ranged from 800-1300 cpms. Filters were exposed to X-ray film (Fuji Medical X-Ray Film) and intensifying screens (Fisher Scientific) for 1-3 days at -80 °C. Plaques showing positive hybridization to the probe were excised and subsequently plaque purified. Pure plaques were stored in 1 ml storage medium (SM; NaCl, MgSO₄, 1M Tris-HCl pH 7.5, and 2% gelatin) and 5 μl chloroform.

Homology screen for first exon of mouse Mel₁₄ receptor

The pcDNA-3 plasmid (1 μl of 100 ng/ml; Invitrogen) containing the 1.1 kb mouse Mel₁₄ receptor cDNA fragment was transformed into DH5α competent cells as described above. Plasmid DNA was isolated by standard technique (modified from Sambrook et al., 1989) and digested with HindIII and XhoI restriction enzymes. The digested DNA was run on a 1.2% agarose gel and visualized with ethidium bromide. The 1.1 kb band corresponding to the mouse Mel₁₄ cDNA insert was excised and purified according to manufacturer's protocol with the GeneClean Kit (Bio101). The purified cDNA was digested with DdeI restriction enzyme to produce a 146 bp fragment containing sequence for the first transmembrane region. The 146 bp fragment was excised, purified, and radiolabeled with α³²-dCTP (3000 Ci/mmol, New England Nuclear; 1.44 x 10⁷ dpms)
using the Prime-A-Gene Kit (Promega). This probe was used in a separate experiment to screen a *P. leucopus* genomic library according to the methods described previously. Plaques showing positive hybridization to the probe were excised and subsequently plaque purified. Pure plaques were stored in 1 ml storage medium (SM; NaCl, MgSO₄, 1M Tris-HCl pH 7.5, and 2% gelatin) and 5 µl chloroform.

**ISOLATION OF PHAGE DNA**

50,000 PFUs (plaque forming units) of phage DNA were incubated with $10^{10}$ KW251 cells. The infected cells were added to NZCM media and incubated at 37°C until cell lysis occurred (6-8 hours). Chloroform was added 15 minutes prior to the end of incubation to promote complete lysis. The solution was then incubated overnight at 4°C in 1M NaCl and 10% PEG and centrifuged at 7000 RPM for 20 minutes. The resulting pellet was resuspended in a solution of 5% Igepal, 3.6 mM CaCl₂, 30 mM Tris, 5 mM MgCl₂, 125 mM KCl, 0.5mM EDTA, 0.25% deoxycholic acid, and 6 mM β-ME and treated with (60 µg/ml) RNase A and (25 µg/ml) DNase I for 30 minutes at 37°C. Phage particles were extracted using chloroform/isoamyl alcohol (C:IAA 24:1) and layered over a glycerol gradient diluted in a solution of 0.5% Igepal, 30mM Tris, 125mM KCl, 0.5mM EDTA, and 14.4M β-ME. After centrifugation at 35,000 RPM, the pellet was resuspended in SM and incubated with 20 mM EDTA, 0.5% SDS, and proteinase K overnight at 55°C to eliminate phage proteins. Phage DNA was extracted with water saturated phenol, phenol/chloroform, and chloroform/isoamyl alcohol (24:1) and precipitated with 3M NaOAc and 100% EtOH. The resulting DNA was stored in a Tris-EDTA buffer.
Southern Blot Analysis

Phage DNA that showed positive hybridization to the full length cDNA probe was digested with each of the following enzymes for 90 minutes at 37 °C in separate reactions: *SalI, EcoRI, XhoI, BamHI, HindIII, and EcoRV*. Phage DNA that hybridized with the 146 bp probe was digested with *BamHI, HindIII, EcoRV, PstI, ClaI, KpnI, SmaI*, and *ApaI* in separate reactions. The digests were visualized on a 1.2% agarose gel containing ethidium bromide. The DNA in the gel was denatured for 30 minutes in a solution of 1.5M NaCl and 0.5M NaOH and neutralized with 0.5M ammonium acetate. DNA was transferred from the gel to a Gene Screen Plus Hybridization Transfer Membrane (NEN Research Products) by capillary action using 2X SSC as a transfer buffer. The transfer membrane was UV crosslinked (Fisher Scientific; optimum setting), incubated 6-8 hours at 42 °C in prehybridization buffer described for Genomic Library Screening, and incubated overnight at 42 °C in hybridization buffer containing the mouse Melia 32P-labeled cDNA probe. The membrane was washed in a solution of 2X SSC, 1% SDS and exposed to X-ray film (Fuji) with an intensifying screen (Fisher Scientific) at -80 °C for 1-2 days.

Subcloning into Bluescript SK+

The restriction digests described for Southern Blot Analysis were repeated. Phage DNA bands corresponding to regions of positive hybridization on the Southern Blots were excised from the gel and purified with the Gene-Clean Kit (Bio-101) according to the manufacturer’s instructions. Bluescript SK+ plasmid DNA (Stratagene) was linearized with the appropriate restriction enzyme, phosphatased with calf intestinal
alkaline phosphatase (Promega), extracted with phenol/chloroform and chloroform/isoamyl alcohol (24:1), and precipitated in 3M NaOAc and 100% EtOH. Phage DNA bands from EcoRI, HindIII, BamHI, and PstI digests were ligated into the plasmid and used to transform DH5α competent cells as described previously. Bacterial colonies containing the recombinant plasmid were harvested and incubated in 50 ml LB and 50 ng/ml ampicillin overnight at 37 °C. Plasmid DNA was extracted from the bacterial cells by standard technique (Sambrook et al., 1989), digested with EcoRI, HindIII, BamHI, or PstI, run on a 1.2% agarose gel stained with ethidium bromide, and visualized under UV light. Glycerol stocks of appropriate transformation reactions were incubated in LB containing 0.05 mg/ml ampicillin overnight at 37 °C and used to extract plasmid DNA via the Qiagen or the Bio-Rad Midi-Prep protocol.

A 2.0 kb subclone that contained exon 2 of the *P. leucopus* *Mel₁α* receptor (see results) was digested at 37°C by Apal, BamHI, ClaI, EcoRI, EcoRV, HindIII, KpnI, SacI, SalI, SmaI, XbaI, and XhoI restriction enzymes in separate reactions to create a restriction map. The digests were visualized on a 1.2% agarose gel stained with ethidium bromide. DNA bands were excised from EcoRI and BamHI digests and subcloned into Bluescript SK+ phagemid as described above.

**SEQUENCING PEROMYSCUS LEUCOPUS MEL₁α RECEPTOR DNA**

Automated sequencing was used to sequence the *Mel₁α* receptor gene from *P. leucopus*. To accomplish this, Bluescript SK+ cloning vector (Invitrogen) containing the *P. leucopus* DNA inserts was amplified and fluorescent-labeled using the Sequitherm Excel II Long-Read DNA Sequencing Kit (Epicentre Technologies) according to
manufacturer's protocol. This sequencing reaction utilizes the dideoxynucleotide termination method of Sanger et al. (1977), except that the primers used are fluorescent labeled and specific for the M13 sequence on the plasmid. Reaction mixes were heated to 95 °C for 5 minutes and subjected to 30 cycles of the following PCR settings: 30 seconds at 95 °C, 15 seconds at 54 °C, and 1 minute at 70 °C. Stop/loading buffer was added to the reaction mixes immediately after completion of the PCR cycles to terminate replication of the plasmid. Sequencing reactions were run on a 4% acrylamide gel using a Li-Cor 4200 automated sequencer. The resulting sequences were compared to sequences published in GenBank (National Library of Medicine) and sequence analysis was performed using the MacVector program (Eastman Kodak).

Results

Genomic Library Screening

*P. leucopus* genomic library plates containing approximately 50,000 plaques per plate were screened at low stringency (30% formamide) with mouse (*Mus musculus*) Mel1a receptor probes for exon 1 and exon 2 in separate experiments. Each probe hybridized to several different plaques, which were excised from the library plates, plaque purified, and stored in storage media. DNA was isolated from the lambda phage and subjected to digestion with several different restriction enzymes as described in the Methods section.
SOUTHERN BLOT ANALYSIS

The low stringency (30%) Southern blot analysis for both of the screening experiments showed hybridization to the Mel$_{1a}$ receptor probes. For the exon 2 screening experiment, one HindIII band at approximately 2.0 kb and three BamHI bands between 1.0 and 2.0 kb hybridized with the full length mouse Mel$_{1a}$ receptor probe. For the exon 1 screening experiment, two PstI bands at 1.6 and 2.0 kb, one HindIII band at 4.0 kb, and one EcoRI band at 5.0 kb hybridized to the 146 bp mouse exon 1 Mel$_{1a}$ receptor probe (Figure 10). These results indicated that homologous sequences to the mouse Mel$_{1a}$ receptor existed within bands containing *P. leucopus* genomic DNA.

SUBCLONING INTO BLUESCRIPT SK+

The bands which hybridized to the mouse Mel$_{1a}$ receptor probes were subcloned into Bluescript SK+ cloning vector (Invitrogen) and plasmid DNA isolated as described in the Methods section. Presence of *P. leucopus* DNA inserts within the multiple cloning site of Bluescript was determined by digesting the plasmid vector with the appropriate restriction enzymes. Visualization of DNA bands that resolved at the expected molecular weights on a 1.2% agarose gel indicated DNA inserts that potentially contained *P. leucopus* Mel$_{1a}$ receptor sequence (data not shown).

SEQUENCE ANALYSIS

Forward and reverse primers from the Sequitherm Excel II Long-Read DNA Sequencing Kit (Epicentre Technologies) were used to generate forward and reverse sequence data for the *P. leucopus* Mel$_{1a}$ receptor (Figure 11). The 2.0 kb HindIII-digested
clone from the exon 2 screening experiment exhibited high homology to all known Mel₁₄ receptor sequences from other species (data not shown). However, the first 107 base pairs from the 5’ region of this clone did not align to the first exon of any known melatonin receptor sequences. Alignment began immediately after the conserved intron/exon 2 border seen in other species, indicating the presence of intron sequence at the 5’ region of the 2.0 kb clone (Figure 11).

In order to fully sequence the 2.0 kb exon 2 clone in both the forward and reverse directions, it was subjected to several separate restriction digests and subcloned into smaller fragments (Figure 12, Table 3). Digestion with EcoRI produced two bands visible by gel electrophoresis: a 3.0 kb band containing 0.7 kb of the 3’ end of exon 2, and a 1.3 kb band containing a 5’ flanking intron sequence and most of exon 2. Digestion with BamHI produced a 0.6 kb band containing the intron sequence and approximately 500 bp of the 5’ end of exon 2, a 1.1 kb band containing the middle region of exon 2, and a 3.5 kb band containing approximately 300 bp of the 5’ end of the clone. The 3.0 and 1.3 kb EcoRI-generated and the 0.6 kb BamHI-generated subclones were isolated and sequenced. As expected, these subclones showed homology to exon 2 of Mel₁₄ receptor sequences from other species. The 1.1 kb and the 3.5 kb BamHI-generated subclones did not transform into DH5α competent cells and could not be isolated and sequenced.

Subcloning the 2.0 kb exon 2 clone allowed an analysis of the 3’-untranslated region (3’-UTR) of the P. leucopus Mel₁₄ receptor (Figure 11). The 3’-UTR contained an ATTTA sequence which may be involved in regulating mRNA stability (Sachs, 1993 in Roca et al., 1996) and several potential polyadenylation sites downstream from the coding region. One of these potential sites, the polyadenylation consensus sequence ATTTAA
(between base pairs 1691 and 1756; Figure 11), is also found in the 3'-UTR of the mouse
(*Mus musculus*) Mel₁₅ receptor (Roca et al., 1996).

The second exon of the *P. leucopus* Mel₁₅ receptor encodes a protein of 289 amino
acids. It has several structural features typical of the melatonin receptor subfamily of
GPRs: an NRY motif immediately downstream from the third transmembrane domain; a
C(C/Y)IHCS motif just downstream from NRY; and an NAXXY motif in transmembrane
domain VII (Figure 13). At the amino acid level, the *P. leucopus* Mel₁₅ receptor exhibits
the greatest degree of homology to two cricetine rodents, the Djungarian hamster (*P.
sungorus*, 94.1% identical) and the Syrian hamster (*M. auratus*, 94.8% identical), and is
least identical to the *Xenopus laevis* Mel₁₅ receptor (66.0% identical).

**Discussion**

*Interspecific comparisons of Mel₁₅ receptors*

Comparisons with other species demonstrate that the gene cloned in this study is
the *P. leucopus* Mel₁₅ receptor. First, a GenBank BLAST query (National Library of
Medicine) revealed high identity between the *P. leucopus* sequence and all other
melatonin receptors sequenced to date in other species (data not shown). It is most
closely related to Mel₁₅ receptors in the Syrian hamster (*Mesocricetus auratus*) and the
Djungarian hamster (*Phodopus sungorus*). Second, the deduced amino acid sequence for
the *P. leucopus* Mel₁₅ receptor shares high amino acid identity with the cloned Mel₁₅
receptors for the Syrian hamster, Siberian hamster, and all other mammals (Figure 13).
Third, the gene structure for the *P. leucopus* Mel₁₅ receptor resembles other melatonin
receptors. It is comprised of two exons with a large (>8 kb in other species; Reppert and
Weaver, 1995) intron between them. The intron splice site is located at the beginning of transmembrane region 2 before the codons encoding for amino acids GN in every melatonin receptor, including *P. leucopus*, sequenced to date (Figure 13; Kokkola and Laitinen, 1998). The second exon contains sequence for transmembrane regions 2-7 and the remainder of the 3’ region of the gene, while the first exon contains the 5’UTR and the first transmembrane region (for review, see Kokkola and Laitinen, 1998; Reppert and Weaver, 1995).

**Future studies**

Cloning of the Mel₁₆ receptor in *P. leucopus* marks the first time this receptor, so critical in the photoperiodic regulation of reproduction, has been isolated in an outbred species that is highly genetically variable in their reproductive response to daylength. Completion of several experiments is necessary to characterize expression of this gene in *P. leucopus*. First, in situ hybridization (ISH), RNAse protection assays (RPA), and RT-PCR can be used to detect Mel₁₆ receptor mRNA levels in *P. leucopus* brain regions. Characterization of mRNA expression in this species will allow comparisons to be made with other mammals that have been investigated, such as the Syrian hamster (Gauer et al., 1998), Siberian hamster (Ebizawa et al., 1994), the laboratory mouse (Roca et al., 1996), human (Reppert et al., 1995), sheep (Ebizawa et al., 1994), and laboratory rat (Ebizawa et al., 1994). Second, mRNA expression patterns between photoresponsive and nonresponsive white-footed mice will be determined by ISH, RPA, and RT-PCR analysis. These results will then be compared with in vitro autoradiography studies that have
established melatonin binding site patterns in photoresponsive and nonresponsive individuals.

Past studies have used in situ hybridization to determine regions of Mel₁₃ receptor mRNA expression in the brain of other mammalian species in which the receptor has been cloned. In situ hybridization allows detection of mRNA in fixed tissue samples. Tissue samples are sectioned, fixed, and hybridized to a labeled (either radioactive or linked to a color detection system) probe complementary the mRNA being investigated. This method can determine precise anatomical regions of mRNA expression and can even detect cell types within a region that have mRNA transcripts (reviewed in Kronenberg et al., 1996). In situ hybridization has consistently shown Mel₁₃ receptor mRNA expression in the rodent suprachiasmatic nuclei (SCN) of the hypothalamus and the pars tuberalis (PT) of the anterior pituitary, prominent sites of IMEL binding and the presumed brain areas for the circadian and reproductive actions of melatonin, respectively (Reppert and Weaver, 1995).

However, in situ hybridization may not detect low levels of mRNA transcripts spread among many cells. RNAse protection assays (RPA) and RT-PCR are both sensitive assays that can detect very low levels of specific mRNA transcripts from total RNA samples extracted from target tissues (see Kronenberg et al., 1996 for a review of these techniques). These procedures may reveal brain areas that exhibit low levels of Mel₁₃ receptor mRNA transcripts that are undetectable by in situ hybridization.

Comparison of Mel₁₃ receptor gene expression between photoresponsive and nonresponsive white-footed mice is vital to our understanding of the mechanism(s) that determine individual variation in photoresponsiveness. Presently, no studies have
investigated the hypothesis that individual variation in photoresponsiveness may be due to individual variation in melatonin receptor transcript levels. The Syrian (*Mesocricetus auratus*) and Siberian (*Phodopus sungorus*) hamsters, species in which the Mel1a receptor has been cloned, exhibit individual variation in photoresponsiveness. However, reproductive nonresponsiveness seems to occur in these animals as the result of variation in their circadian systems (Loudon et al., 1998; Puchalski and Lynch, 1986, 1988, 1991, 1994; Ralph and Menaker, 1988; Shimomura and Menaker, 1997; Stirland et al., 1996a, 1996b).

*P. leucopus* is highly genetically variable in its reproductive response to photoperiod (Heideman and Bronson, 1991; Heideman et al., 1999b; Lynch et al., 1981). Although the mechanism(s) for this variation is not clear, it has been established that differences in the circadian system do not account for variation in photoresponsiveness (see results in Chapter Two; also see Carlson et al., 1989). These results, in conjunction with studies that have determined that melatonin administration has differential effects on the gonads of responsive and nonresponsive mice (Carlson et al., 1989; Heath and Lynch, 1982), indicate that reproductive nonresponsiveness may result from differences in the melatonin effector pathway (Lynch et al., 1982). A potential source of variation in the melatonin effector pathway may be melatonin receptor abundance and distribution. Weaver et al. (1990) showed no differences in melatonin binding sites in the brains of responsive and nonresponsive mice, but their study lacked the statistical power to detect differences (Heideman et al., 1999). In contrast, Heideman et al. (1999a) showed differences in melatonin binding sites within the medial preoptic area (MPOA) and bed nucleus of the stria terminalis (BNST) between photoresponsive and nonresponsive mice.
It is unknown if Mel1a receptor mRNA levels exhibit a similar pattern of individual variation within this species. A future objective based on work completed during this project is to determine if differences in Mel1a receptor mRNA expression exist in photoresponsive and nonresponsive white-footed mice.

**Conclusion**

This study reports the partial cloning of the Mel1a receptor in *Peromyscus leucopus* for the first time. The receptor exhibits high identity with all known melatonin receptors to dates, especially those rodent species from the sub family *Cricetinae*. Future studies will establish receptor expression using in situ hybridization and ribonuclease protection assay techniques. These techniques will be used to determine if differences in melatonin receptor gene expression exist between photoresponsive and nonresponsive white-footed mice.
LITERATURE CITED


Reppert., S.M., Godson, C., Mahle, C.D., Weaver, D.R., Slaughenhaupt, S.A., and J.F.


Table 1. The effect of short day (SD), long day (LD), and constant darkness (DD) on duration (alpha), phase angle\(^*\), and free running period (tau) of wheel running activity for responsive (R) and nonresponsive (NR) mice. Sample sizes are in parentheses. Values presented as means ± SE in hours.

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Alpha (h)</th>
<th>Phase Angle (h)</th>
<th>Tau (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Short Day</td>
<td>Long Day</td>
<td>Short Day</td>
</tr>
<tr>
<td>R males</td>
<td>14.31 ± 0.36 (14)</td>
<td>8.51 ± 0.22 (15)</td>
<td>-0.52 ± 0.16 (14)</td>
</tr>
<tr>
<td>NR males</td>
<td>14.68 ± 0.34 (13)</td>
<td>8.32 ± 0.26 (12)</td>
<td>-0.37 ± 0.12 (5)</td>
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<tr>
<td>R females</td>
<td>14.22 ± 0.40 (16)</td>
<td>8.11 ± 0.14 (19)</td>
<td>-0.72 ± 0.14 (11)</td>
</tr>
<tr>
<td>NR females</td>
<td>14.26 ± 0.47 (10)</td>
<td>8.26 ± 0.14 (13)</td>
<td>-0.68 ± 0.33 (5)</td>
</tr>
</tbody>
</table>

Total Male Mean 14.49 ± (27) 8.43 ± (27) -0.48 ± (19) -0.17 ± (28) 23.81 ± (25)
Total Female Mean 14.23 ± (26) 8.17 ± (32) -0.71 ± (16) -0.38 ± (24) 23.94 ± (29)
Total R Mean 14.26 ± (30) 8.28 ± (25) -0.61 ± (25) -0.25 ± (33) 23.75 ± (33)
Total NR Mean 14.50 ± (23) 8.29 ± (34) -0.53 ± (10) -0.28 ± (19) 24.08 ± (21)

\(^*\) Phase angle is defined as the onset of activity relative to lights off. A negative value means activity started after lights off.

\(*\) Significantly different from responsive females, p = 0.0003.

\(**\) Significantly different from males, p = 0.0424.

\(***\) Significantly different from responsive mice, p = 0.0082.
Table 2.  R-square and P-values from correlation analyses of circadian characters and pubertal state in male mice from the unselected control line.

<table>
<thead>
<tr>
<th></th>
<th>Testis Index (L x W)</th>
<th>Body Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Free-Running Period</td>
<td>( r^2 = 0.059 )  ( p = 0.365 )</td>
<td>( r^2 = 0.024 )  ( p = 0.564 )</td>
</tr>
<tr>
<td>Short Day Alpha</td>
<td>( r^2 = 0.134 )  ( p = 0.298 )</td>
<td>( r^2 = 0.025 )  ( p = 0.661 )</td>
</tr>
<tr>
<td>Short Day Phase Angle</td>
<td>( r^2 = 0.137 )  ( p = 0.326 )</td>
<td>( r^2 = 0.034 )  ( p = 0.636 )</td>
</tr>
<tr>
<td>Long Day Alpha</td>
<td>( r^2 = 0.005 )  ( p = 0.809 )</td>
<td>( r^2 = 0.130 )  ( p = 0.187 )</td>
</tr>
<tr>
<td>Long Day Phase Angle</td>
<td>( r^2 = 0.002 )  ( p = 0.877 )</td>
<td>( r^2 = 0.108 )  ( p = 0.252 )</td>
</tr>
<tr>
<td>Clone Name</td>
<td>Vector</td>
<td>Length (base pairs)</td>
</tr>
<tr>
<td>------------</td>
<td>------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>Mel₁₄HindIII-1</td>
<td>Bluescript SK+</td>
<td>2000 bp</td>
</tr>
<tr>
<td>Mel₁₄HindIII-2</td>
<td>Bluescript SK+</td>
<td>2000 bp</td>
</tr>
<tr>
<td>Mel₁₄EcoRI-1</td>
<td>Bluescript SK+</td>
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<tr>
<td>Mel₁₄EcoRI-2</td>
<td>Bluescript SK+</td>
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<tr>
<td>Mel₁₄BamHI-1</td>
<td>Bluescript SK+</td>
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Table 4. Minimum differences in circadian characters detectable between responsive and nonresponsive mice from sample sizes used in experiments (based on post-hoc power analyses, $P = 0.8$, 0.05 level of significance).

<table>
<thead>
<tr>
<th></th>
<th>Free-Running Period</th>
<th>Short Day Alpha</th>
<th>Short Day Phase Angle</th>
<th>Long Day Alpha</th>
<th>Long Day Phase Angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>0.358 h</td>
<td>0.919 h</td>
<td>0.380 h</td>
<td>0.594 h</td>
<td>0.122 h</td>
</tr>
<tr>
<td>Females</td>
<td>0.215 h</td>
<td>1.08 h</td>
<td>0.414 h</td>
<td>0.362 h</td>
<td>0.313 h</td>
</tr>
</tbody>
</table>
Figure 1. Schematic diagram of the effect of brief pulses of light (A-E) on the phase of the circadian activity rhythm. The activity rhythm of a single individual exposed to constant darkness for 65 days is shown twice (double-plotted) to aid in visual inspection of the data. Pulses B and D, which occurred in the early subjective night, induced phase delays. Pulses C and E, which occurred in the late subjective night, induced phase advances. Pulse A fell during the subjective day and had no effect of the the circadian activity rhythm.
Figure 2. Representative running wheel activity records of responsive and nonresponsive mice exposed to short day (SD), long day (LD) and constant darkness (DD). Bars at bottom of records indicate light cycles, with solid bar representing period of darkness. Recording errors resulted in missing activity values for #2011, 2017, and 2003.
Free-running period (tau) of activity of responsive and nonresponsive mice exposed to constant darkness. Data presented as means ± SE. Different letters denote significant differences between means.

Figure 3.
Figure 4. Duration (A) and phase angle (B) of activity of responsive and nonresponsive mice exposed to short days. Negative hour values in (B) indicate activity onset after lights off. Data presented as means ± SE. Different letters denote significant differences between means.
Figure 5. Duration (A) and phase angle (B) of activity of responsive and nonresponsive mice exposed to long days. Negative hour values in (B) indicate activity onset after lights off. Data presented as means ± SE. Different letters denote significant differences between means.
Figure 6. Free-running period (tau) of locomotor activity vs. testis index (A) and body weight (B) in male mice from the unselected control line.
Figure 7. Paired testis weights (A) and paired seminal vesicle weights (B) of responsive and nonresponsive male mice exposed to constant darkness (DD) and short days (SD). Data presented as means ± SE. Different letters denote significant differences between means.
Figure 8.  Paired ovary weights (A) and uterine weights (B) of responsive and nonresponsive female mice exposed to constant darkness (DD) or short days (SD). Data presented as means ± SE. Different letters denote significant differences between means.
Figure 9. Body weights of male (A) and female (B) mice exposed to constant darkness (DD) and short days (SD). Data presented as means ± SE. Different letters denote significant differences between means.
Figure 10. Example of the Southern blot technique used to locate and clone the *P. leucopus* Mel-1a receptor gene. *P. leucopus* DNA from the restriction digest (A) was transferred onto a nitrocellulose membrane and incubated with radiolabeled *Mus musculus* Mel-1a receptor probe. Autoradiography revealed probe hybridization to several DNA fragments on the blot (B). These fragments were subcloned and sequenced.
Figure 11. Nucleotide sequence of the second exon of the *P. leucopus* Mel1a receptor gene. The sequence is numbered starting from the 5' flanking intron sequence. In the coding region, the presumed transmembrane domains are underlined. The stop codon for translation (TAA) is designated with an asterisk. In the 3' untranslated region, ATTTA sequences are underlined and potential polyadenylation sites are in boldface.
Figure 12. Schematic diagram of the *P. leucopus* Mel1a receptor (upper portion) and genomic clones of the gene (lower rectangles). Names of the restriction enzymes used in cloning each fragment are noted next to the clones. Arrows indicate amount of the clones sequenced in the forward and reverse directions. Gray areas denote intron sequences.
Figure 13. Comparison of the deduced amino acid sequence of the *P. leucopus* Mel-1a receptor (second exon) to Mel-1a receptors in other mammalian and non-mammalian species. The presumed transmembrane domains are underlined. Asterisks represent stop codons for translation. *P. sungorus* = Djungarian hamster; *M. auratus* = Syrian hamster; *M. musculus* = laboratory mouse; *R. norvegicus* = laboratory rat; *H. sapiens* = human; *G. gallus* = chicken; *X. laevis* = African clawed frog.
Vita

Sean Bradford Majoy