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Evolutionary and Practical Implications of Pseudo-Estrus Behavior in Florida Panthers (Puma Concolor Coryi)

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Evolutionary and Practical Implications of Pseudo-Estrus Behavior in Florida Panthers (*Puma concolor coryi*)

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Abstract - Estrus behavior by females for reasons other than reproduction (pseudo-estrus) has been reported in species of primates and felids, and alternative hypotheses have been put forth to explain its evolution and function. We observed 3 separate cases of pseudo-estrus behavior by 2 *Puma concolor coryi* (Florida Panther) females while they were nursing young (<1 month old) kittens. We used VHF and GPS telemetry data, genetic pedigree analysis, and visual observations to provide insight into the evolutionary and practical implications of this behavior for Panthers. We suggest that female Panthers likely consort with males while nursing kittens to maintain amicable relations with these males to prevent infanticide. For studies monitoring Puma dens with radio-telemetry, pseudo-estrus events may be confused with litter abandonment, and thus our observations are useful to field biologists who may consider removing kittens from the wild following presumed abandonment events to prevent kitten mortality.

Pseudo-estrus can be defined as estrus behavior exhibited by females outside of potentially fertile periods (Sommer et al. 1992), or more generally, as estrus behavior for reasons other than reproduction. In many species of primates, sexual receptivity and copulation are not strictly correlated with ovulation (Heape 1900, Hrdy 1979). With *Presbytis entellus* Dufresne (Hanuman Langurs), pregnant females often mate with unfamiliar males when they approach or enter a troop (Hrdy 1977). The function of this behavior could be to avoid infanticide by confusing paternity, which might allow new males to tolerate offspring sired by other males (Hrdy 1977). Alternatively, females may copulate during pregnancy to deplete sperm available for other females within the troop to reduce future resource competition (Sommer et al. 1992).

In felids, pseudo-estrus has been reported in *Panthera leo* L. (African Lions; Packer and Pusey 1983, Schaller 1972) and *Puma concolor* L. (Puma; Logan and Sweanor 2001). Female Lions have been visually observed copulating during pregnancy and while lactating with small cubs (Schaller 1972), although the behavior appears to be relatively rare (Packer and Pusey 1983). Schaller (1972) noted that a female Lion may sometimes appease a potentially aggressive male by copulating with him. For Pumas, where direct observation of copulation is unlikely, radio-telemetry has been used to document females consorting (and presumably copulating) with males while pregnant and also while nursing kittens (Logan and Sweanor 2001). Similar to the earlier explanations for Langurs and Lions, Logan and Sweanor (2001) hypothesized that female Pumas may exhibit pseudo-estrus to engage males in breeding unions to confuse paternity or reinforce pair bonds to reduce the possibility of infanticide.

We documented 3 cases of pseudo-estrus behavior by 2 female *P.c. coryi* Nelson and Goldman (Florida Panthers) who were nursing young (<1 month old) kittens, both directly (by visual and auditory observation) and indirectly (using radio-telemetry). We used these observations to provide insight into the evolution and function of pseudo-estrus behavior for Pumas. We also believe our observations have important practical

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implications for field biologists studying Pumas because male-female associations during kitten rearing may be confused with litter abandonment. For Puma populations where the fate of individual animals is important to local or regional stakeholders, there may be significant pressure to remove kittens from the wild if abandonment is suspected. For threatened or endangered populations, such as Florida Panthers (federally endangered in the United States), the potential to negatively affect kitten recruitment by permanently removing offspring from the wild is also an important consideration. Our observations provide Puma biologists and managers with behavioral information that should aid in making decisions about kitten removal when abandonment is suspected.

Methods. We located Panther dens and handled kittens according to methods described by Benson et al. (2008) and Land et al. (1998). We left a remote telemetry system, accessed by cellular phone, near dens that allowed us to remotely monitor the presence and absence of adult females at dens (Land et al. 1998). We located radio-collared Panthers 3 times weekly from a fixed-wing aircraft, and our mean telemetry location error was 123.9 m (SE = 13.9, n = 45 stationary test collars located; Land et al. 2008). We also used ground-based telemetry to locate Panthers when feasible. We considered male and female Panthers to be associating when aerial or ground telemetry locations were indistinguishable during simultaneous locations. Finally, one Panther described below was fitted with a store-on-board GPS radio-collar that provided additional location data once the collar was recovered. We used the results of paternity analysis from a genetic study of Florida Panthers (Johnson et al. 2010) to attempt to identify the sires of Panther kittens. All observations and data collection took place on the Florida Panther National Wildlife Refuge (FPNWR) in southwest Florida.

Studies of Panther denning behavior indicate that females spend ≥45% of their time at the den site during the denning period and do not leave the den unattended for ≥36 hours during at least the first 4 weeks following parturition (Florida Fish and Wildlife Conservation Commission, Naples, FL, unpubl. data; Maehr et al. 1989, 1990). The observations described below involved denning females <2–3 weeks following parturition, which is usually a period of intensive den attendance by Panthers followed by increased time away from the den later in the denning period (Maehr et al. 1989). With the exception of the observations described below, Panthers resumed normal denning behavior following den visits and handling of kittens from 1992 to present.

Observation #1. On 15 March 2005 we handled 2 kittens at a den in a litter produced by FP107, a 5-year-old female Panther. During the next 2 telemetry flights (16 and 18 March), FP107 was located with adult male FP131 2.7 and 0.4 km away from the den site, respectively. On 19 March, we investigated on the ground and found male and female tracks and scrapes in the area of the den indicating that a male and female Panther had been traveling side-by-side on a nearby trail. It was apparent that FP107 had not returned to the den site because the ground had not been recently disturbed. Both kittens were alive but had lost 300 g (approximately 20% of their weight) since our initial visit. Due to the endangered status of the Panther population, we decided to supplementally feed the kittens with kitten milk replacer (KMR), which is available commercially. Our remote telemetry system indicated that she did not return to the den during that night (19 March) or the next morning, and we located her approximately 3.2 km south of the den by aerial telemetry on the morning of 20 March. Given her continued absence from the den, her association with a male Panther, and the deteriorating condition of the kittens, we believed she had abandoned the den and that the kittens' prospects for survival were poor. We removed the kittens from the wild late in the morning on 20 March and transported them to the Jacksonville Zoo in northeast Florida with the knowledge that kittens of this

age would not be candidates for a return to the wild. During the next flight, FP107 was located consorting with a different adult male (FP119). Paternity analysis was inconclusive as both males that FP107 associated with during this period were potential sires.

Observation #2. On 25 March 2007, we visited the den of 5-year-old female Panther FP113, where we captured and handled 3 kittens that were approximately 7 days old. We set up a remote telemetry system at the den and also used a combination of aerial, ground, and GPS telemetry to reconstruct the movements of FP113 in late March and early April. She left the den site on 27 March, and telemetry data indicated she did not return until 4 April. We located her in the company of a 3-year-old radio-collared male Panther (FP154) during all aerial and ground telemetry locations obtained between 30 March-3 April (n = 3 locations). These locations were 2.8, 4.5, and 6.7 km from the den site. During this time, we became concerned that the kittens could have died or that FP113 might have abandoned the kittens. We revisited the den site 4 times between 30 March and 3 April and found all 3 kittens alive during each visit. On 30 March, the kittens' weights had increased by 100–125 g from their weights at our initial visit (925–1050 g); by 3 April, the kittens' weights were 45–50 g less than their initial weights, and their condition and demeanor appeared to have deteriorated. We attempted supplemental feeding with KMR during 3 revisits, and the kittens ingested increasing amounts of milk during these visits (range: <1 cc to ≤35 cc). On 4 April, FP113 was detected at the den site at 0400 hours (the time at which the VHF beacon activated), indicating that she had returned to the den sometime during the night or early morning. She resumed normal denning behavior after returning, and we believe that at least 2 of the 3 kittens survived to independence because we obtained photos of her with 2 dependent kittens at approximately 7 and 20 months after the kittens were born. Average age of independence for Panther kittens is just over 1 year (mean = 397 days, SD = 75 days, n = 35), and survival of radio-collared kittens ≥6 months to independence is extremely high (Florida Fish and Wildlife Conservation Commission, Naples, FL, unpubl. data). We cannot rule out that our supplemental feeding enhanced the survival of these kittens during the period when the female was away from the den; however, we believe they would have survived without the KMR as the kittens ingested <1 cc of KMR prior to our most successful feeding efforts which took place <24 hours prior to her return to the den. Subsequent genetic analysis identified FP154 as the sire of this litter of kittens.

Observation #3. In late March 2009, FP113 began exhibiting potential denning behavior by restricting her movements, so we investigated on the ground. On 8 April, we located FP113 using ground telemetry to investigate further, and she was not in the area of the suspected den site. FP113 was moving around and making "yowling" calls characteristic of female Panthers in estrus. At one point she came closer to our observer, who made a Panther "whistle" call. FP113 whistled in return and the observer saw FP113 walk past making softer "yowling" calls. It appeared as if FP113 did not detect the presence of the observer. After she was out of sight and appeared to be stationary, she began "caterwauling" loudly. Caterwauling is a vocalization made by adult female Pumas during estrus and probably indicates breeding readiness (Logan and Sweanor 2001). Caterwauling by female Pumas has been observed during male-female associations and by lone females, probably to aid in locating a mate (Logan and Sweanor 2001; J. Benson, M. Lotz, E. Land, and D. Onorato, pers. observ.). Yowling is thought to be used by male and females Pumas for a variety of functions including sexual identity and sexual advertisement (Logan and Sweanor 2001) and has been observed in females suspected of being in estrus when in close proximity to males (J. Benson, M. Lotz, E. Land, and D. Onorato, pers. observ.). Based on the behavior of FP113 on 8 April, we assumed she was in estrus and was likely not denning with neonatal kittens. However, on 28 July 2009, we obtained a photograph from a remote camera that showed FP113 with 1 kitten that we estimated to

be approximately 3-4 months old. Regardless of the exact age of the kitten, it was clearly born either before or soon after the observations we made on 8 April, indicating that she was displaying estrus behavior, either while pregnant or (more likely) after giving birth.

Theoretical implications. At least 2 main hypotheses have been suggested to explain pseudo-estrus behavior in mammals. One possibility, the infanticide defense hypothesis, is that females may mate with males while pregnant or nursing to prevent incoming males from killing the offspring by confusing paternity or by exhibiting estrus-behavior to keep males from discovering offspring (Hrdy 1979, Logan and Sweanor 2000). Sommer et al. (1992) rejected this hypothesis for Langurs because: 1) they don't discriminate between "harmless" males (sires) and potentially infanticidal males (new males dispersing into the area) when exhibiting pseudo-estrus, and 2) most infanticide victims were subsequently killed by males that had copulated with females displaying pseudo-estrus. Thus, Sommer et al. (1992) suggested that a more likely explanation was that pseudo-estrus was a manifestation of female-female competition for sperm. By depleting sperm of reproductive males, a female might reduce successful fertilization in other females in a troop, and thereby reduce subsequent competition for resources as she rears her offspring (Sommer et al. 1992).

We believe our observations with Panthers (particularly observation #2, for which we obtained the most detailed information) are more likely explained by the infanticide defense hypothesis. Female Pumas disperse less frequently and for shorter distances than males (Anderson et al. 1992, Maehr et al. 2002, Sweanor et al. 2000), consistent with most species of polygynous mammals (Greenwood 1980). Female Florida Panthers often exhibit philopatry and establish home ranges that overlap with those of their mother (Maehr et al. 2002), similar to female Pumas in western United States populations (Lindzey et al. 1994, Ross and Jalkotzy 1992, Sweanor et al. 2000). By tolerating female offspring within or adjacent to their home ranges, female Pumas are likely facilitating easier and more rapid establishment of a breeding range by their female offspring and accruing inclusive fitness benefits. In fact, FP113 had established her breeding range within that of her mother's on FPNWR, where all of our observations took place. Presumably this behavior is dependent on the availability of sufficient resources in the local area to provide successful breeding habitat to her offspring without compromising her own ability to produce and raise future offspring. As resources appeared to be sufficient on the FPNWR to allow for female philopatry, engaging in sperm competition with neighboring females, at the cost of neglecting the provisioning and care of young offspring, would be unlikely to increase fitness. Thus, by engaging in sperm competition, female Pumas would potentially be reducing both direct and indirect fitness benefits by increasing mortality risk to their offspring and competing with close relatives.

In contrast, the infanticide defense hypothesis is supported by our observations, especially observation #2. Female Panthers that detect males in the vicinity of a natal den site might intercept these males and display pseudo-estrus to keep them from discovering the kittens and/or to establish and maintain amicable relations to confuse paternity. Genetic analysis identified FP154 as the sire of FP113's March 2007 litter, which might suggest he would be unlikely to kill these kittens. Nonetheless, we still believe that FP113's association with this male for 5+ days while neglecting 1-2 week old kittens is best explained in the context of avoiding infanticide. Sommer et al. (1992) considered sires to be "harmless" to Langur offspring; however, differences in the social systems of Langurs and Panthers may explain this discrepancy. Whereas Langurs are social animals living in troops where members, and especially mates, would be expected to recognize each other and possibly their offspring, Panthers are solitary, and associations between females and males are relatively rare and short in duration. Moreover,

Panthers often mate with several males during true estrus periods, making it likely that both males and females do not know the true sire of offspring. Indeed, FP113 was detected associating with another radiocollared male (FP119) during a telemetry flight in December 2006, approximately 90 days (the length of gestation for Panthers) prior to giving birth to the kittens described in observation #2. Based on this telemetry data, we believed FP119 was the sire until genetic analysis identified FP154 as the true sire. We assume she copulated with both males (and potentially others) during her estrus period in December 2006. Thus, when she encountered FP154 post-parturition, it's reasonable to assume that neither Panther was sure who the sire was, and the safest strategy for FP113 was to treat FP154 as a potential infanticide threat. Given that FP154 was relatively young for a breeding male Panther at 3 years old, it's also likely that FP113 and FP154 did not have an extensive history of interactions, which may have also increased the risk of infanticide. In areas of lower Puma density, where males may have more exclusive access to breeding females or for older Pumas that may have a long history of interactions, it is possible that a female would not display pseudo-estrus in the presence of a mate, as infanticide would be less likely. As noted by Logan and Sweanor (2001), associations between males and females during estrus and pseudo-estrus could result in tolerance of a female and her kittens during subsequent meetings as well and thus be beneficial to female survival and reproductive success.

Practical Implications. We decided to remove the kittens discussed in observation #1 because we believed they had been abandoned and that they were unlikely to survive. During the events of observation #2, we also considered the possibility of removing the kittens as they began to lose weight and became lethargic. FP113's continued absence from the den and her association with a male Panther suggested to us that she could be abandoning the kittens. Alternatively, we discussed whether pseudo-estrus, as observed by Logan and Sweanor (2001), could explain FP113's association with FP154. Thus, we were presented with a difficult decision between risk of kitten mortality, and associated public relations concerns, if we left the kittens in the wild or loss of potential recruits to the population if we intervened. Hands-on research and management of Panthers in south Florida is a delicate enterprise that requires balancing pressures from the opinions of the many stakeholders with the challenges of incorporating knowledge of Panther ecology and behavior into effective conservation biology. Our observations may be valuable to other Puma biologists and wildlife managers that encounter similar situations in the future because they show that females may leave young kittens to consort with males for multiple days and then return to continue raising them successfully. Thus, when a nursing female is observed associating with males away from the den site, or simply stays away from the kittens for multiple days, it should not be automatically assumed that she is abandoning the kittens. In cases when risk of death to kittens is unacceptable (e.g., for public relations reasons), careful monitoring and supplemental feeding of kittens with KMR could be used to mitigate the risk of death during the female's absence. It should be noted that anytime a female leaves young kittens unattended for multiple days, their chance of death is increased; thus, we recognize that decisions about removal should be case-specific and require careful consideration of the ethical, conservation, and public relations implications. We hope that our observations provide useful information to aid such decisions.

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