

EVOLUTION OF INDUCED OVULATION IN NORTH AMERICAN CARNIVORES

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We tested the hypothesis that induced ovulation is adaptive in North American carnivores by providing a mechanism to overcome the risk of unsuccessful mating in solitary species living in seasonal environments and a method for females to evaluate male quality via sexual selection inside the reproductive tract. We obtained published data on North American carnivores and determined from their distribution a coefficient of seasonality and primary productivity. Using traditional statistics and comparative methods, we determined that induced ovulators lived in more seasonal environments apparently not influenced by energy. No statistical differences in behavioral traits existed between induced and noninduced ovulators, but trends in data were consistent with our predictions, with induced ovulators tending to have larger home ranges and longer estrous periods. Mating systems also differed between the groups: induced ovulators were characterized by mostly (93%) multimale mating systems, whereas noninduced ovulators were monogamous (42%), multemale (33%), or polygynous (25%). Also, induced ovulators exhibited larger sexual dimorphism and smaller neonates than noninduced ovulators or felids. We suggest that induced ovulation evolved through sexual selection as a reproductive strategy beneficial for males (assurance of egg fertilization during short pair bonds) and females (postcopulatory mate choice based on level of stimulation causing induced ovulation).

Seasonality (i.e., variation in environmental conditions and primary productivity within a year) is an important evolutionary pressure affecting life history, behavior, and reproduction of animals (Boyce 1979). For example, animals living in seasonal environments must give birth and raise young when conditions are favorable. In northern latitudes, the favorable season may be short (often <4–5 months). Thus, early parturition allows for maximum offspring growth and higher survival.

Parturition of most mammals living at high latitudes occurs in spring. In species with fixed gestation periods, mating is a

critical factor that determines timing of parturition. However, numerous species of carnivores have evolved delayed implantation, a reproductive strategy that allows the uncoupling of mating and parturition (Ferguson et al. 1996; Sandell 1990). In North American carnivores, it appears that delayed implantation also may have evolved to allow mating when conditions are better for encountering mates, suggesting some evolutionary pressures due to sexual selection.

For solitary species that occupy large home ranges, seasonality and short breeding seasons provide additional constraints, and these constraints are gender specific. For example, males of species that pair dur-

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ing reproduction (e.g., red fox, *Vulpes vulpes*) or species that live in groups (e.g., gray wolf, *Canis lupus*) can monitor the reproductive status of females, and copulation easily can occur during ovulation. However, in solitary species that are promiscuous (e.g., wolverine, *Gulo gulo*), short pair bonds may not allow males to assess whether a female already has ovulated and bred or whether ovulation has yet to occur. Waiting for a female to ovulate may preclude males from finding and breeding with additional females and thus directly decrease fitness. Furthermore, males may risk losing paternity if females subsequently breed with other males. Mate guarding would prevent this problem, but time spent guarding results in lost opportunities for additional breeding attempts. Consequently, duration of pair bonds may represent a compromise for males between number of mates and certainty of paternity.

Short pair bonds also constrain sexual selection by females. For example, in species that pair or live in groups, females easily may assess genotypic quality of males via phenotypic displays. However, in solitary species, females encounter only 1 male at a time, and simultaneous comparisons (through sexual display or physical competitions among males) may not occur. Thus, selective pressures should favor development of alternative ways for females to evaluate genotypic quality of males, possibly via postcopulatory mechanisms (e.g., sperm selection) or via morphology associated with mating (e.g., size of erect penis or baculum, or stimulation level associated with copulation).

Induced ovulation is a process by which eggs are released after behavioral, hormonal, or physical stimulation (Milligan 1974; Taymor 1978). Because subminimal stimulation does not induce ovulation (Colby 1970), certain attributes of male genital organs such as penile spines (Stoddart 1979) may increase the odds of inducing ovulation (Zarrow and Clark 1968). In the Mammalia, induced ovulation has been demon-

strated for lagomorphs (Staples 1967), rodents (Chitty and Austin 1957; Gray et al. 1974), marsupials (Crawford et al. 1998; Smith 1994), and carnivores (Boone et al. 1998; Colby 1970). However, not all species within a family are induced ovulators, suggesting that selection pressures may have differed for various species.

In this study, we test several hypotheses related to the evolution of induced ovulation. Our primary hypothesis is that induced ovulation evolved in species living in low-energy (i.e., primary productivity) and highly seasonal environments. Low energy would result in decreased population density and greater home-range size as adaptations to obtain necessary requisites for life processes. Seasonality would act as a primary selective force shaping behavioral and life-history traits (Ferguson et al. 1996).

According to bet-hedging theory, if the environment is unpredictable or at least if juvenile survival responds more strongly to environmental conditions than does adult survival, the best option for a parent is to keep its own survival high and its reproductive effort low (Both et al. 1999; Lindström 1999). Unpredictability of the environment is intensified by time delay between reproductive decisions made by the mother and environmental conditions that offspring face at birth. Hence, we predict that species with induced ovulation inhabit seasonal environments, invest less in each reproductive event (e.g., short gestation and small neonates), and are relatively long lived (maintain high adult survival) compared with species without induced ovulation.

We tested our predictions using data on North American carnivores. North American carnivores are well known both morphologically and physiologically, and climatic conditions within North America provide a high contrast of seasonality (Ferguson et al. 1996). We used comparative methods because species may not represent independent data points (Harvey and Pagel 1991; Harvey et al. 1995). However, not all

factors are constrained by phylogeny. For example, variation in patterns of habitat selection may be explained best at the species level; thus, comparative analyses controlling for genus or family effects may do little in explaining variation. Because behavioral plasticity may allow individuals within the same species to inhabit different environments and use different behavioral strategies, comparative analyses may not reflect species variability as well as traditional nonphylogenetic methods. Thus, we used both comparative method (Garland et al. 1993) and conventional statistics depending on the phylogenetic level that explained most variation in species' traits.

METHODS

We used the phylogenetic tree proposed by Bininda-Emonds et al. (1999) and the taxonomy of Wozencraft (1993) with 2 exceptions. First, we considered skunks as a separate family, the Mephitidae (Dragoo and Honeycutt 1997). Second, we considered spotted skunks (*Spilogale*) as consisting of 3 species: western spotted skunk (*S. gracilis*), eastern spotted skunk (*S. putorius*), and pygmy spotted skunk (*S. pygmaea*). The data consisted of 9 families, 21 genera, and 35 species of North American terrestrial carnivores (Larivière and Ferguson 2002: appendix 1).

Data on life-history (mating system, weaning age, gestation length, neonate mass, age at maturity, litter size, interbirth interval, longevity, and sexual dimorphism), behavioral (density, home range, and duration of estrus), and environmental correlates were taken from Ferguson and Larivière (2002), whereas information on induced ovulation (Larivière and Ferguson 2002: Appendix 1) was supplemented by reviews on carnivore reproduction (Colby 1974; Milligan 1982; Weir and Rowlands 1973; Wright 1963), acknowledging that empirical confirmation of induced ovulation is only available for a few species such as the American mink (*Mustela vison*—Enders 1952; Hansson 1947), striped skunk (*Mephitis mephitis*—Wade-Smith and Richmond 1978), wolverine (Mead et al. 1993), and black bear (*Ursus americanus*—Boone et al. 1998). Copulation rates were determined from the same published sources for the following species: *Ursus americanus*, 3 copulations/day;

Gulo gulo, 4 copulations/day; *Martes americana*, 3 copulations/day; *Martes pennanti*, 1 copulation/day; *Mustela erminea*, 3 copulations/day; *Mustela nivalis*, 3 copulations/day; *Leopardus pardalis*, 10 copulations/day; *Lynx rufus*, 5 copulations/day; *Panthera onca*, 100 copulations/day; and *Puma concolor*, 70 copulations/day. To normalize distribution, data were log transformed (base 10) before analysis.

Statistical analyses.—We used Monte Carlo algorithms to incorporate phylogenetic structure (i.e., phylogenetic tree) in order to estimate statistical parameters for phylogenetic analysis of covariance (ANCOVA—Garland et al. 1993). We obtained initial limits corresponding to life-history and behavioral traits from the average of all species values. We performed simulations according to the gradual model of speciation that assumes variance changes are proportional to branch lengths. For each simulated data set ($n = 1,000$), we calculated phylogenetically corrected estimates of ANCOVA parameters using general linear models.

We tested the prediction that induced ovulators have life-history and behavioral traits that are different from those of noninduced ovulators and felids. Felids were found to be statistical outliers (Larivière and Ferguson 2002) and were treated as a separate group. We calculated conventional ANCOVA statistics from observed sample data and compared them with distribution of simulated test statistics. ANCOVA adjusts for differences associated with body mass between groups and enabled us to assess differences in traits due to groups alone (i.e., variation in body mass has been statistically removed from the analysis). These adjusted trait values are known as least-square means and represent predicted mean values for traits after regressing traits on body mass for each group. The ANCOVA model used type III sum of squares to determine statistical difference between least-square (adjusted) means associated with each group. The phylogenetically corrected critical value of differences due to group (induced ovulators, noninduced ovulators, and felids) was set at $\alpha = 0.05$ from the 95th percentile of the simulated distribution. We report significant differences in least-square means that control for body size variation using Tukey's multiple comparison tests.

Mating systems are often coded as categorical data, although the information also can be inter-

preted as coarse information on an underlying continuous variable (Garland et al. 1993). Polygyny, promiscuity, and monogamy can be considered groupings along a continuum from breeding group size >5 for highly polygynous species to breeding group size of 3–5 for weakly polygynous species associated with multimale mating systems to breeding group size of 1–2 for monogamous species (Clutton-Brock et al. 1980). Hence, we rescored the mating system data as 3-category ordered variables: 3 = polygyny, 2 = multimale, and 1 = monogamy. Standardized contrasts were computed from the mating system coding, and ANCOVA was used to control body size effects. We used female mass as a covariate to control for effect of body size on sexual size dimorphism and thus mating system (Loison et al. 1999).

Phylogeny was obtained from 35 species (2 polytomies). We tested whether differences in life-history and behavioral traits occurred among carnivores with induced ovulation, carnivores that do not have induced ovulation, and felids with induced ovulation. We tested the null hypothesis of no difference among the 3 groups by phylogenetically corrected ANCOVA.

Phylogenetic corrections are necessary when variation in the observed data set is due to phylogenetic structure, creating nonindependence of data points (Harvey and Pagel 1991). We tested for the hierarchical pattern of variation in life-history and behavioral traits using nested analysis of variance (ANOVA) for 3 taxonomic levels (species, genus, and family) to determine the level that accounted for most of the variability in traits (Harvey and Pagel 1991). We assume that major variation at the genus and family levels indicates the need for phylogenetic correction methods. Conversely, major variation at the species levels indicates that phylogenetic correction may not be necessary.

RESULTS

There were differences among traits as to which phylogenetic level explained most of the variation (Table 1). Variation in environmental attributes (primary productivity and seasonality) and all behavioral traits except copulation rate was explained best at the species level (Table 1). In contrast, variation in most life-history traits was greater at the family level, except for longevity and

TABLE 1.—Comparison of relative variance attributable to species ($n = 35$), genera ($n = 21$), and family ($n = 9$) level of 8 life-history and 7 behavioral traits for species of North American carnivores from nested analysis of variance. Asterisks indicate phylogenetic level where most variation is observed.

	Percentage of total variance		
	Family	Genera	Species
Environmental attributes			
Primary productivity	0.9	4.3	94.8*
Seasonality	29.8	2.4	68.2*
Behavioral traits			
Population density	1.0	9.5	89.5*
Female home range	3.8	25.8	70.4*
Duration of estrus	7.9	22.5	69.6*
Male home range	16.3	19.9	63.8*
Copulation rate	60.9*	39.1	0.0
Life history traits			
Mating system	88.8*	11.2	0.0
Weaning duration	64.5*	2.0	33.5
Gestation length	61.3*	11.6	27.1
Neonate mass	52.2*	37.1	10.6
Age at maturity	51.2*	5.3	43.5
Litter size	48.1*	32.3	19.5
Interbirth interval	47.9*	6.0	46.1
Longevity	42.3	4.7	53.0*
Sexual dimorphism	21.3	4.4	74.3*

sexual dimorphism. These results indicate that phylogenetic correction methods may not be necessary for all traits. Nested ANOVA provides a suggestion of the taxonomic level that should be used for analysis (Harvey and Pagel 1991). Consequently, we used the results on conventional ANCOVA for traits that varied at the species level and phylogenetically corrected analyses for traits that varied mostly at the family level.

Environmental, behavioral, and life-history attributes.—We predicted that induced ovulation evolved in highly seasonal environments characterized by low primary productivity. However, only seasonality differed between induced ovulators, noninduced ovulators, and felids (Table 2). Overall, felids and noninduced ovulators lived in

TABLE 2.—Analysis of covariance (ANCOVA) tests of difference among noninduced ovulators, induced ovulators, and felids for 13 life-history and behavioral traits from 35 species of North American carnivores with induced ovulation (IO) or without induced ovulation (no-IO). The covariate is female body mass except in the case of male home-range size, in which male body mass is the covariate. Models of evolutionary change were no phylogenetic change (conventional ANCOVA) or gradual evolutionary change (proportional to branch lengths). Asterisks indicate statistically significant differences. Least-square mean values within a row are assigned the same letter if they do not differ statistically.

	Conventional ANCOVA			Least-square means			Phylogenetic		
	<i>n</i>	Observed <i>F</i>	Critical <i>F</i>	<i>P</i>	Induced ovulators		Felids	<i>F</i>	<i>P</i>
					Noninduced ovulators	Induced ovulators			
Environmental attributes									
Primary productivity	35	2.16	2.86	0.14	1,032 a	990 a	1,218 a	36.2	>0.20
Seasonality	35	7.46	2.86	0.002*	0.91 a	1.12 b	0.76 a	43.0	>0.20
Behavioral traits									
Population density	33	0.35	2.90	0.71	1.01 a	0.67 a	0.48 a	36.5	>0.20
Female home range	31	1.00	2.88	0.38	7.1 a	15.0 a	5.8 a	38.0	>0.20
Duration of estrus	30	0.54	2.92	0.59	4.9 a	8.5 a	7.3 a	56.2	>0.20
Male home range	31	0.70	2.88	0.50 ^b	8.0 a	15.3 a	15.3 a	27.3	>0.20
Copulation rate	11	6.05	3.59	0.04	—	3.0 a	20.1 b	30.4	>0.20
Life-history traits									
Mating system	35	21.0	2.86	0.0001 ^b	1.30 ^c a	2.05 b	2.05 b	19.7	0.04*
Weaning duration	33	1.75	2.90	0.19	67.8 a	91.8 a	58.7 a	37.3	>0.20
Gestation length	35	8.27	2.86	0.001	53.6 a	43.6 b	68.2 c	17.6	<0.25
Neonate mass	34	18.8	2.88	0.0001	97.7 a	51.6 b	146.2 c	20.0	0.06*
Age at maturity	34	3.02	2.88	0.06	409 a	540 a	673 b	37.0	>0.20
Litter size	35	8.09	2.86	0.002 ^b	4.3 a	3.3 a	2.2 b	40.6	>0.20
Interbirth interval	34	4.52	2.88	0.02	365 a	446 b	343 a	41.9	>0.20
Longevity	33	0.00	2.90	0.99	4,571 a	4,571 a	4,571 a	49.3	>0.20
Sexual dimorphism	35	5.01	2.86	0.013*	1.23 a	1.55 b	1.33 ab	25.7	>0.20

^a Significant interaction between male mass and reproductive category (IO, no-IO, and felids).

^b Slopes differ significantly among groups.

^c Mating system scored as polygyny = 3, multimale = 2, and monogamy = 1.

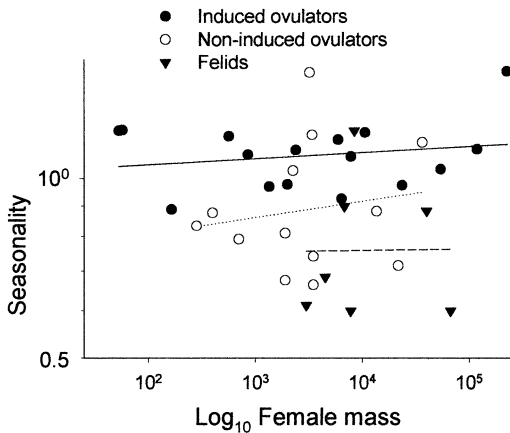


FIG. 1.—Seasonality in the distribution ranges of North American carnivores that are induced ovulators (excluding felids), noninduced ovulators, or felids ($n = 35$ species). Lines represent ordinary least-square regression for each group.

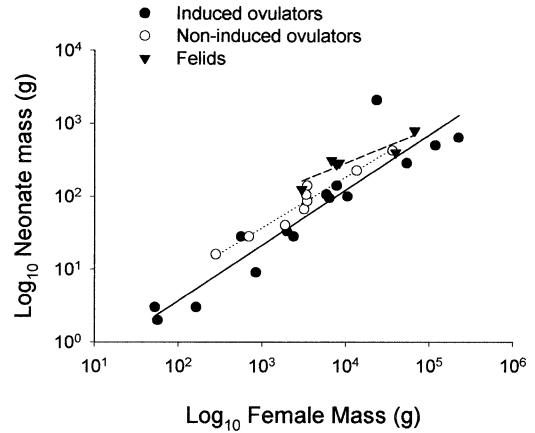


FIG. 2.—Variation in neonate mass among North American carnivores that are induced ovulators (excluding felids), noninduced ovulators, and felids. Lines represent ordinary least-square regression for each group.

less seasonal environments compared with induced ovulators (Table 2; Fig. 1).

We predicted that species with induced ovulation lived at lower population density, were wide ranging (i.e., larger male and female home ranges), had a longer estrous period (to overcome the uncertainty of finding a mate), and had a greater copulation rate (to overcome the uncertainty of fertilization). There were no differences among groups in any of the behavioral traits, although there was a trend for induced ovulators to have larger home ranges and longer estrous periods (Table 2).

Our primary assumption is that induced ovulation benefits females by enabling them to assess male quality during copulation. For this competition to occur, females must accept multiple mates; thus, we predicted that induced ovulators predominantly would display multimale mating systems. As predicted, mating system differed among the 3 groups with all felids (100%) and most (93%) species with induced ovulation having multimale mating system (Table 2). In comparison, species with spontaneous ovulation had a more even distribution of monogamous (42%), multimale

(33%), and polygynous (25%) mating systems.

Weaning age, gestation length, age at maturity, litter size, interbirth interval, and longevity did not differ among induced ovulators, noninduced ovulators, and felids (Table 2). However, neonate mass differed among groups ($P = 0.06$), with offspring size being smallest for induced ovulators and largest for felids (Table 2; Fig. 2). Induced ovulators also were characterized by greater sexual dimorphism compared with noninduced ovulators (Table 2; Fig. 3).

DISCUSSION

Comparative versus conventional analyses.—Whether phylogenetic corrections are necessary depends on the distribution of variation among the hierarchical levels of phylogeny. In comparative analysis of life-history evolution, statistical interpretations of general linear models (e.g., ANCOVA) are confounded by lack of independence among data points resulting from common ancestry of taxa (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991). Efforts to statistically control for phylogenetic effects are plagued by the same problem as trying to separate the effects of genetics and en-

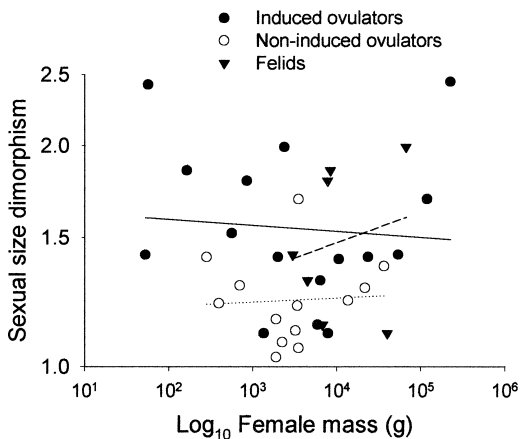


FIG. 3.—Variation in sexual dimorphism among North American carnivores that are induced ovulators (excluding felids), noninduced ovulators, and felids. Lines represent ordinary least-square regression for each group.

vironment (Brown 1999). Conservative interpretation of conventional comparisons that include consideration of taxonomical hierarchy and simple data transformations can provide reasonable insight into evolutionary processes without phylogenetic corrections (Freckleton 2000; Ricklefs and Starck 1996).

Trait values are not necessarily very similar between pairs of closely related species (Pagel 1999; Price 1997; Ricklefs and Stark 1996). For example, we found significant differences in seasonality between induced and noninduced ovulators using conventional methods that control for allometric differences due to body size. However, phylogenetic corrections indicated that evolutionary differences in seasonality of environments inhabited by induced and noninduced ovulators is not unusually large compared with variation in environmental seasonality within groups. Still, real and detectable differences occurred in descendants of each group. Nested ANOVA indicated that the majority (68%) of variation in seasonality of environments inhabited by carnivore species occurs at the species level. This result indicates that species have evolved specific adaptations to particular

habitats and that the use of phylogenetic corrections to account for variation at the family level is overly conservative.

Nested ANOVA indicated that for some traits, a large component of variation is not due to shared ancestry. Such characters may vary so much that they are of no use in systematics. Conversely, the same traits can be used in comparative ecological studies without any precautions with regard to phylogeny. We argue that nested ANOVA can help to decide whether data can be used as they stand or whether comparative methods are required (Bjorklund 1997). We argue that for traits that have the majority of variation at the species level, the assumption that species are independent is reasonable and use of phylogenetic corrections is overly conservative. Hence, use of comparative methods for all comparisons as a conservative strategy is problematic due to the restrictive assumptions (Ricklefs and Starck 1996).

Environmental, behavioral, and life-history correlates and their impacts on carnivore reproduction.—Seasonal environments pose an evolutionary challenge to animals living therein. Because the season favorable to reproduction is short, timing of reproduction is under great evolutionary pressure. In North American carnivores, we found evidence suggesting that induced ovulation evolved in seasonal environments because species with induced ovulation typically lived in more variable environments when compared with species without induced ovulation. Seasonality is a strong force driving the evolution of carnivores. Because of changes in environmental conditions, animals must adapt to overcome such challenges. Thus, animals inhabiting seasonal environments exhibit numerous adaptations in behavior (Murray and Boutin 1991) or morphology (Murray and Larivière 2002). Similarly, induced ovulation in seasonal environments may provide numerous advantages. First, it alleviates the need for mates to meet during the short temporal window of a fixed ovulation period. Sec-

ond, induced ovulation may be especially beneficial for females when juvenile mortality is high. In seasonal environments, females that lose their 1st litter could mate again within a short interval and still give birth during optimal environmental conditions. In numerous species such as the raccoon (*Procyon lotor*), females may bear a 2nd litter if the 1st is lost. However, females will only bear a 2nd litter if the 1st is lost at or soon after birth (Sanderson and Nalbandov 1973). This is consistent with the importance of timing parturition during optimal environmental conditions (Ferguson et al. 1996; Sandell 1990).

We also predicted that induced ovulators were solitary and wide ranging (Greenwald 1956; Llewellyn and Enders 1954). If such is the case, then fertilization could occur when both sexes meet, and this would be especially valuable when such encounters are infrequent. Our data set on North American carnivores provided little support for this hypothesis. For example, we could not detect any statistical differences in population density or home-range size among induced ovulators, felids, and noninduced ovulators. Possibly, such differences may have been undetected because of the low power of the small data set. This is suggested by observed trends that are consistent with our predictions that species with induced ovulations have larger home ranges and lower population density than noninduced ovulators (Table 2). Furthermore, a trend also was observed for longer estrous period in induced versus noninduced ovulators. Nonetheless, variation in behavioral traits occurred mostly at the family level, precluding the use of traditional statistics for phylogenetically corrected methods. Possibly, variation in such behavioral traits among populations within a species contributed to our inability to detect differences. Finally, because we suspect that the baculum may be used to remove sperm plugs deposited by previous males, we predicted that copulation rate should be higher in induced versus noninduced ovulators. How-

ever, our data did not allow for comparisons because of lack of data for noninduced ovulators.

For sexual selection to occur inside the reproductive tract (for example, via sperm competition), females must accept several males. Thus, induced ovulators should display multimale mating systems to allow sexual selection to occur within the female reproductive tract. This hypothesis is supported by our analyses: induced ovulators were characterized by mostly multimale mating systems, whereas noninduced ovulators were monogamous, multimale, or polygynous.

This last finding provides an entirely new enigma of mammalian reproduction. For example, whereas it may be easy to understand the benefit of induced ovulation for males, female benefits are not as obvious. When encountering a single male during breeding season, females have a choice of mating or not mating with the male encountered. However, few matings are random, and the sex that invests the most in reproduction (e.g., females for most mammals) is typically "choosy." However, females encountering males sequentially may not be able to assess male quality by simultaneous comparisons. In this case, selection inside the female tract via sperm selection or sexual stimulation may allow a female to gather information in order to compare several males simultaneously. In mammalian carnivores, baculum size increases with age (Miller et al. 1998). Because age is an indicator of genotypic quality (reflecting greater survival ability), we believe that females use baculum size as an indicator of mate quality and induced ovulation as a mechanism to bear offspring from the best possible mates. There is already evidence that greater stimulation is required to induce ovulation in already mated females (Adams 1981). Thus, females that breed with "good" males risk little by copulating with younger males. Similarly, females risk little by initially copulating with small males because older

males are likely to provide enough stimulation to cause abortion of the 1st set of eggs and induced ovulation of a second set. In some cases, multiple paternity may occur (e.g., *Ursus americanus*—Schenck and Kovacs 1995), suggesting again that secondary copulations may succeed in causing abortions or new ovulations.

In this study, we have considered the Felidae separately from other induced ovulators. Felids branched off early from the rest of the carnivores, and the split between Feliformia (felidlike carnivores) and Caniformia (canidlike carnivores) occurred 40×10^6 years ago (Bininda-Emonds et al. 1999). This early lineage split may explain why felids have peculiar reproductive characteristics such as induced ovulation (Foster 1977; Schramm et al. 1994) and yet live mostly in low-seasonality environments (Table 2), have small bacula in relation to body size (the smallest in the Carnivora—Dixson 1995; Larivière and Ferguson 2002), and have extremely high copulation rates. Possibly, felids may compensate for their lack of baculum by increasing copulation rate (Ewer 1973). In some species of felids such as lions (*Panthera leo*), high copulatory rates may increase odds of paternity. Thus, even though lions form prides, individuals may benefit from increased penile vigor and numerous copulations for competition inside the female tract. This would still allow females to choose mates even within a pride where males are viewed as being of equal value (Schramm et al. 1994). Although paternity and copulation rates have not been linked, it is possible that males who caused most stimulation probably sire most offspring. Finally, because the simple presence of new males may cause abortions in already mated females, induced ovulation may speed the process of gestation, which would have great advantages for males who may not control prides for long periods.

Induced ovulation and bet hedging in seasonal environments.—Lifetime reproduction represents a compromise between

yearly energy expenditure and expected future opportunities. Animals inhabiting highly seasonal environments may maximize their lifelong reproductive success by adopting a bet-hedging strategy, whereby animals overcome the uncertainty of environmental conditions by spreading their reproductive efforts over several years and investing less in each yearly attempt (smaller litter size and smaller neonate mass). Using the comparative method, we detected a significant difference only for neonate mass, with induced ovulators giving birth to smaller neonates compared with either non-induced ovulators or felids. Other traits such as gestation, litter size, and interbirth interval were not different statistically, but trends in data were in the direction predicted: induced ovulators tended to have shorter gestation, smaller litters, and greater interbirth intervals, thus indicating a bet-hedging strategy. Longevity, however, was similar for all 3 groups.

Apart from the functions detailed previously, induced ovulation also may provide means to reduce female costs associated with forced copulation by males. For example, young and immature males may not succeed in intra- or intersexual displays, but they may nonetheless attempt sneaky or forced copulation. Should forced copulation occur, females may be able to avoid bearing offspring from the forced copulation event by subsequently breeding with a “better” male. Although forced copulation is poorly documented in nonhuman mammals, the sexual size dimorphism of most carnivore species suggests that it may occur in the wild (Miller et al. 1996). In agreement with this hypothesis, our analyses showed that North American carnivores with induced ovulation were characterized by greater sexual size dimorphism compared with noninduced ovulators. Thus, induced ovulation may not only allow females to evaluate male quality inside the reproductive tract but also may provide females with a defense against forced copulation and overall more control over the paternity of their

offspring compared with spontaneous ovulators. However, this explanation will remain a hypothesis until we learn more about frequency of forced copulations in mammals and aspects of sexual selection inside the mammalian female tract.

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