

Postpartum and Lactational Estrus: A Comparative Analysis in Rodentia

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Virgin rodents exhibiting cycling estrus have traditionally been used for comparative studies of reproductive behavior. However estrus occurs in other life-history contexts, some of which differ from cycling estrus (CE) in that (a) the female is disposed to behave both maternally and sexually and (b) they result in litter overlap (i.e., the simultaneous gestation and lactation of two litters). In this report, two of these other modes of estrus are examined, with emphasis on their evolutionary and ecological implications. By means of a literature search of the order Rodentia, postpartum estrus (PPE) and lactational estrus (LE) were documented in 15 families, 71 genera, and 141 species. Analysis of these data showed that PPE and LE were nonrandomly distributed across taxa. They were statistically overrepresented in the family Cricetidae and underrepresented in squirrels (Sciuridae) and in pocket mice and kangaroo rats (Heteromyidae). Analysis of the phenotypes by which PPE and LE are achieved suggests important differences between them and CE in several parameters of female reproductive effort and breeding strategy, including maternal and copulatory behavior, optimal timing of litters, and hormonal control of heat and lactation.

Comparative psychologists have focused on the cycling virgin estrus of rodents as a model system (e.g., Feder, 1981). As a result, evolutionary interpretations of reproductive patterns also center on this particular example of sexual heat (e.g., Adler, 1978; Dewsbury, 1975, 1981, 1982a, 1982b; Patterson & Thaeler, 1982). However, in the wild estrus is not limited to females exhibiting ovarian cycles, much less to females at a virgin cycling estrus. Estrus and mating occur in a number of life-history contexts. Cycling estrus (CE) is preceded by one or more ovarian cycles and may occur at the virgin heat, at the first heat of a season, at the first heat after weaning a litter, or after the loss of a suckling litter.

In contrast, postpartum estrus (PPE) and lactational estrus (LE) are not immediately preceded by an ovarian cycle. They also occur prior to weaning and therefore raise new questions about the reproductive strategies of female rodents. These new questions have not been systematically addressed despite recent experimental attention from comparative psychologists (Bean & Estep, 1981; Beasley, Johnston, & Zucker, 1981; J. Connor & Davis, 1980a, 1980b; Dewsbury, 1979a, 1979b; Dewsbury, Evans, & Webster, 1979; Gilbert, 1982; Gilbert, Pelchat, & Adler, 1980, in press; Hedricks & McClintock, in press).

The most striking feature of PPE and LE is litter overlap, the simultaneous gestation and lactation of two litters. Overlapped breeding potentially brings both costs and benefits to a female. By reducing the interval between litters, it increases the number of offspring she can produce in a season or lifetime. On the other hand, it may introduce energetic and behavioral conflict between the overlapped litters and complicate the female's apportionment of parental investment. Understanding these potential consequences may reveal the

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adaptive nature of the control and timing of all forms of estrus.

This article provides the basis for a new comparative examination of female breeding strategies by drawing together the data on PPE and LE. I also examine this new data base for evolutionary and ecological patterns in rodent reproduction.

Phyletic Distribution of Postpartum and Lactational Estrus

Postpartum estrus occurs within 1 or 2 days of parturition (Hoffmann & Schwartz, 1965). Lactational estrus takes place 2 or more days into lactation, but prior to weaning (Gilbert, 1982). The temporal distinction between PPE and LE is an empirical one, based on the observation that when nursing suppresses estrus, it does so only after 1–2 days postpartum and often permits a postpartum heat (e.g., *Rattus norvegicus*, Long & Evans, 1922). In some species postpartum mating is followed by delayed implantation (Aitken, 1977), which may be proportional to the number of suckling young (as in *Mus musculus*, Brambell, 1937; *Clethrionomys glareolus*, Gustafsson, Andersson, & Westlin, 1980; *R. norvegicus*, Weichert, 1940).

Method

The presence or absence of postpartum estrus, lactational estrus, and delayed implantation was determined from the literature. The criteria for evidence were conservative, and as a result not all claims in the literature (e.g., for the presence of postpartum mating) meet the present standards. Litter overlap may be inferred from (a) a simultaneously pregnant and lactating female or (b) intervals between litters that approximate gestation length. These criteria imply the existence of PPE or LE but do not specify which. The demonstration of a particular mechanism of litter overlap (postpartum or lactational mating) requires more detailed observation. Postpartum mating can be inferred by (a) observation of postpartum copulation, (b) a copulatory plug in the vagina within 2 days of parturition, (c) accumulated breeding data in which intervals between litters equal minimum gestation length, or (c) timed matings (male removed no later than 2 days after parturition). Lactational estrus is inferred when (a) a female mates during lactation, (b) vaginal smears during lactation indicate cytological estrus, or (c) when dissections show that ovulation has occurred 2 or more days into lactation. Delayed implantation is inferred when lactational gestations are significantly longer than gestations not accom-

panied by lactation. This inference is strengthened when the length of the delay is positively correlated with the number of suckling young.

Species were included in the data base (Table 1) when there was evidence of lactational gestation, PPE or LE. The data were tested against the hypothesis that litter overlap is randomly distributed at the family and subfamily levels. Species abundances and taxonomic groupings follow Anderson (1967). Chi-square analyses were used, and smaller taxa were collapsed in order to meet the sample size requirements of the test (Siegel, 1956)

Results

PPE, LE, or lactational pregnancy (which implies PPE or LE) was found in 15 rodent families (45% of all families), but only 71 genera (20%) and 141 species (8%) (Table 1). The 141 species with overlap were not randomly distributed among families but were relatively overrepresented in the Cricetidae and underrepresented in the Sciuridae, Echimyidae, and Heteromyidae (Table 2). The Muridae and the remaining 28 families as a group were close to the random expectation.

A closer analysis of the family Cricetidae (Table 3) showed that species with PPE and LE were not randomly distributed across subfamilies. The overrepresentation of litter overlap in the Cricetidae is attributable to its exceptionally high incidence in the Microtinae, relative to the Cricetinae and Gerbillinae.

In the Sciuridae, in which PPE and LE were relatively underrepresented, all six genera with overlap were arboreal (*Aethosciurus*, *Exilisciurus*, *Funisciurus*, *Paraxerus*, *Sciurus*, *Tamiasciurus*). No ground-dwelling forms were found to have litter overlap.

It was long believed that litter overlap was absent from the Sciuridae (Asdell, 1964) despite data in the Russian literature on *Sciurus vulgaris* (Formozov, 1932, cited in Ognev, 1966). Soon after Conaway (1968) reported litter overlap in the Malaysian squirrel *Exilisciurus exilis*, Millar (1970) discovered postpartum breeding in the common American red squirrel *Tamiasciurus hudsonicus*. It has since been described in the African bush squirrel *Paraxerus cepapi cepapi* (Viljoen, 1977) and in the African rain forest squirrels *Aethosciu-*

Table 1
Rodent Species Exhibiting Litter Overlap

Family/Species	PPE	LE	DI	Source
Abrocomidae				
<i>Abrocoma cinerea</i>				Pearson, 1951
Caviidae				
<i>Cavia aperea</i>	+	+	-	Rood & Weir, 1970
<i>C. cutleri</i>	+			Castle & Wright, 1916
<i>C. porcellus</i>	+			Boling, Blandau, Wilson, & Young, 1939
<i>C. rufescens</i>	+			Ubisch & Mello, 1940
<i>Galea musteloides</i>	+	-		Rood & Weir, 1970
<i>Microcavia australis</i>	+			Rood & Weir, 1970
Chinchillidae				
<i>Lagidium peruanum</i>	+			Pearson, 1949
Cricetidae				
Cricetinae				
<i>Baiomys taylori</i>	+		-	Hudson, 1974
<i>Calomys callosus</i>	+			Justines & Johnson, 1970
<i>C. ducilla</i>				Morrison, Dieterich, & Preston, 1976
<i>Mystromys albicaudatus</i>	+			Hall, Persing, White, & Ricketts, 1967
<i>Neotoma albigula</i>				Richardson, 1943
<i>N. cinerea</i>	+	-	-	Egoscue, 1962
<i>N. floridana</i>				Finley, 1958
<i>N. l. lepida</i>	+?			A. Fleming, 1979
<i>N. phenax</i>				Jones & Genoways, 1978
<i>Ochrotomys n. nuttalli</i>	+			Goodpaster & Hoffmeister, 1954
<i>Onychomys leucogaster</i>	+	-	+	Egoscue, 1960
<i>O. torridus</i>	+		-	Taylor, 1968
<i>Oryzomys laticeps</i>	+		-?	Worth, 1967
<i>O. longicaudatus</i>				Pine, Miller, & Schamberger, 1979
<i>O. palustris</i>	+			Svihla, 1931
<i>Ototylomys phyllotis</i>	+		-	Helm, 1975
<i>Peromyscus boylei</i>				Jameson, 1953
<i>P. californicus</i>				Rood, 1966
<i>P. crinitus</i>				Rood, 1966
<i>P. eremicus</i>				Rood, 1966
<i>P. floridanus</i>				Rood, 1966
<i>P. g. gossypinus</i>	+		+	Pournelle, 1952
<i>P. interparvialis</i>	+			Brand & Ryckman, 1968
<i>P. leucopus</i>	+	-	+	Layne, 1968; Hill, 1972
<i>P. maniculatus</i>				Jameson, 1953
<i>P. polionotus</i>				Rood, 1966
<i>P. yucatanicus</i>	+?		+?	Lackey, 1976
<i>Phodopus sungurus</i>	+			Pogosianz & Sokova, 1967
<i>Phyllotis micropus</i>				Pine et al., 1979
<i>Reithrodontomys montanus</i>				Leraas, 1938
<i>Scotinomys teguina</i>	+		-	Hooper & Carleton, 1976
<i>S. xerampelinus</i>	+		+	Hooper & Carleton, 1976
<i>Sigmodon h. hispidus</i>	+		-	Meyer & Meyer, 1944
<i>Tylomys nudicaudus</i>	+		-	Helm & Dalby, 1975
<i>T. panamensis</i>	+		-	Helm & Dalby, 1975
<i>Zygodontomys brevicauda</i>	+			Worth, 1967
Microtinae				
<i>Arvicola richardsoni</i>	+	+?		Jannett, Jannett, & Richmond, 1979
<i>A. terrestris</i>	+			Blake, 1982
<i>Clethrionomys gapperi</i>				Merritt & Merritt, 1978
<i>C. glareolus</i>	+		+	Gustafsson, Andersson, & Westlin, 1980
<i>C. rutilus</i>				Morrison et al., 1976
<i>Dicrostonyx groenlandicus</i>	+		+	Manning, 1954
<i>D. stevensoni</i>				Morrison et al., 1976
<i>Lagurus lagurus</i>	+		-?	Whitney & Burdick, 1966
<i>Lemmus lemmus</i>				Morrison et al., 1976

Table 1 (continued)

Family/Species	PPE	LE	DI	Source
<i>L. sibiricus</i>				Morrison et al., 1976
<i>L. trimucronatus</i>	+			Mullen, 1968
<i>Microtus abbreviatus</i>				Morrison et al., 1976
<i>M. agrestis</i>	+	+	+	Breed, 1969
<i>M. californicus</i>				Greenwald, 1957
<i>M. miurus muriei</i>				Morrison et al., 1976
<i>M. montanus</i>	+			Negus & Pinter, 1965
<i>M. oeconomys</i>				Morrison et al., 1976
<i>M. ochrogaster</i>	+	+	-?	Richmond & Conaway, 1969a, 1969b
<i>M. oregoni</i>	+	-?	-	Cowan & Arsenault, 1954
<i>M. pennsylvanicus</i>	+	-	-	Lee & Horvath, 1969
<i>M. pinetorum</i>	+		-	Kirkpatrick & Valentine, 1970
<i>M. townsendii</i>	+			MacFarlane & Taylor, 1982
<i>Phenacomys longicaudus</i>			+	Hamilton, 1962
<i>P. silvicola</i>				Brown, 1964
<i>Synaptomys cooperi</i>	+			P. Connor, 1959
Gerbillinae				
<i>Desmodillus auricularis</i>				Keogh, 1973
<i>Meriones crassus</i>	+		+	Marafie, Nayak, & Al-Zaid, 1978
<i>M. hurrianae</i>	+			Kaul & Ramaswami, 1969
<i>M. unguiculatus</i>	+	-	+	Meckley & Ginther, 1973; Norris & Adams, 1971
<i>Psammomys o. obesus</i>				Strasser, 1968
<i>Tatera indica</i>	+	-	+	Bland, 1969
<i>T. leucogaster</i>	+			Choate, 1972
Dasyproctidae				
<i>Dasyprocta punctata</i>	+			Smythe, 1978
<i>Myoprocta pratti</i>	+	+	-?	Kleiman, 1970
Dipodidae				
<i>Dipus sagitta</i>				Fenuk & Kazantzzeva, 1937
Echimyidae				
<i>Proechimys guairae</i>	+		-	Weir, 1973; Lusty & Seaton, 1978
<i>P. semispinosus</i>				T. Fleming, 1971
Geomyidae				
<i>Thomomys bottae navus</i>				Miller, 1946
<i>T. perpallidus</i>				Moore, 1929
<i>T. quadratus</i>				Wight, 1930
<i>T. townsendii</i>				Horn, 1923
Heteromyidae				
<i>Dipodomys merriami</i>				Bradley & Mauer, 1971
<i>Perognathus parvus</i>				Speth, Pritchett, & Jorgensen, 1968
Muridae				
<i>Acomys cahirinus</i>	+			Strasser, 1968
<i>A. spinosimus</i>	+			Choate, 1972
<i>Aethomys chrysophilus</i>	+			Choate, 1972
<i>A. namaquensis</i>	+			Choate, 1972
<i>Deomys ferrugineus</i>				Kingdon, 1974
<i>Grammomys s. surdaster</i>	+	+	-	Bland, 1973
<i>Hylomyscus stella</i>	+			Delany, 1971
<i>Hydromys chrysogaster</i>	+	-	+	Olsen, 1982
<i>Leggadina delacatula</i>				Taylor & Horner, 1970a
<i>Lemniscomys striatus</i>				Neal, 1977
<i>Lophuromys flavopunctatus</i>	+			Delany, 1971
<i>Melomys cervinipes</i>				Taylor & Horner, 1970b
<i>M. rufescens</i>				Dwyer, 1975
<i>Mesembriomys gouldii</i>	+	-?	-?	Crichton, 1969
<i>Mus bactrianus</i>	+		+	C. Green, 1932
<i>M. musculoides</i>				Anadu, 1976
<i>M. musculus</i>	+	-	+	Long & Mark, 1911
<i>Notomys alexis</i>	+	+	+	Breed, 1979
<i>N. mitchelli</i>	+			M. Happold, 1976a

(table continues)

Table 1 (continued)

Family/Species	PPE	LE	DI	Source
<i>Otomys irroratus</i>				R. Davis & Meester, 1981
<i>Pogonomelomys sevia</i>	+			Dwyer, 1975
<i>Praomys morio</i>	+			Delany, 1971
<i>P. tullbergi</i>	+			D. Happold, 1978
<i>Pseudomys albocinereus</i>	+			M. Happold, 1976a
<i>P. desertor</i>	+			M. Happold, 1976b
<i>P. gracilicaudatus</i>	+			Fox & Kemper, 1982
<i>P. nanus</i>				Watts, 1979
<i>P. hermannsburgensis</i>	+	-	+	Finlayson, 1941
<i>P. novaehollandiae</i>	+	-	+	Kemper, 1976
<i>Rattus assimilus</i>				Taylor, 1961
<i>R. c. cutchicus</i>				Prakash, Rana, & Jain, 1973
<i>R. (Mastomys) erythro-leucus</i>	+	+		Brambell & Davis, 1941
<i>R. exulans</i>				Wirtz, 1973
<i>R. f. fuscipes</i>				Taylor & Horner, 1973
<i>R. l. lutreolus</i>	+	+		Taylor & Horner, 1973
<i>R. natalensis</i>	+	-	+	Johnston & Oliff, 1954
<i>R. norvegicus</i>	+		+	Long & Evans, 1922
<i>R. rattus</i>				Ewer, 1971
<i>R. s. sordidus</i>				Taylor & Horner, 1973
<i>R. verecundus</i>	+			Dwyer, 1975
<i>Rhabdomys pumilio</i>				Brooks, 1982
<i>Zelotomys woosnami</i>	+			Birkenstock & Nel, 1977
<i>Zyzomys argurus</i>				Watts, 1979
Myocastoridae				
<i>Myocaster coypu</i>				Newson, 1966
Pedetidae	+			
<i>Pedetes surdaster</i>				Coe, 1969
Rhizomyidae				
<i>Tachyoryctes splendens</i>				Jarvis, 1969, 1973
Sciuridae				
<i>Aethosciurus poensis</i>				Emmons, 1979
<i>Exilisciurus exilis</i>				Conaway, 1968
<i>Funisciurus lemniscatus</i>				Emmons, 1979
<i>F. isabella</i>				Emmons, 1979
<i>Paraxerus c. cepapi</i>				Viljoen, 1977
<i>Sciurus vulgaris</i>				Ognev, 1966
<i>Tamiasciurus hudsonicus</i>				Millar, 1970
Zapodidae				
<i>Zapus hudsonius</i>				Quimby, 1951

Note. The presence (+) and absence (-) of postpartum estrus (PPE), lactational estrus (LE), and delayed implantation (DI) are noted when possible. A question mark indicates a tentative designation due to small sample size or ambiguity in the literature source.

rus poensis, *Funisciurus lemniscatus*, and *F. isabella* (Emmons, 1979).

A separate analysis was made of the species comprising the suborder Hystricomorpha (Anderson, 1967). The distribution of litter overlap among hystricomorph species, genera, and families was similar to that of the rodents as an order (Table 4). Suggestions of PPE in five additional hystricomorph species (Weir, 1967, 1974) were not accompanied by data meeting the present criteria for evidence. If these species were included, however, the hystricomorphs would resemble nonhystrico-

morphs even more closely (species 10%, genera 22%, families 47%).

Breeding Phenotypes

The preceding analysis concerned the phyletic distribution of PPE and LE but did not treat PPE separately from LE. A related approach analyzes these as distinct proximal mechanisms, along with delayed implantation. It asks: Are these traits found in one or several combinations (phenotypes)? The existence of only one phenotype might imply a monophyletic origin for

Table 2
Species Distribution of Postpartum and Lactational Estrus Among Families

Family	Expected	Observed*
Cricetidae	47.3	68
Sciuridae	21.8	7
Heteromyidae	6.2	2
Echimyidae	3.6	2
Muridae	38.1	43
All 28 others	24.0	19

Note. $\chi^2 = 24.33, p < .001$.
* $n = 141$ species.

this breeding tactic, whereas several phenotypes might imply repeated, independent evolution and a complex set of selection pressures. In this section the possible phenotypes are contrasted with those actually found in the literature.

Method

Postpartum estrus, lactational estrus, and delayed implantation in their various combinations yield seven potential phenotypes (summarized in Table 5). Only phenotypes A-D have postpartum estrus. Phenotypes A and B have no lactational estrus; A has delayed implantation, B does not. Phenotypes C and D have lactational estrus; C has delayed implantation, D does not. Phenotypes E and F do not have postpartum estrus but do have lactational estrus. Phenotype E has delayed implantation, F does not. Phenotype G, with neither postpartum estrus nor lactational estrus, is physiologically precluded from overlapping its litters.

When all three traits are known, a species can be assigned to a breeding phenotype. The actual distribution of phenotypes was calculated from Table 1.

Results

Only 22 (16%) of the surveyed species could be assigned to phenotypes (Table 5). Nevertheless, a range of phenotypes was found. Phenotype A was the most commonly documented—it is the familiar phenotype of *Rattus norvegicus* and *Mus musculus*. Phenotype B, similar to A but

Table 3
Species Distribution of Postpartum and Lactational Estrus in Cricetidae by Subfamily

Subfamily	Expected	Observed*
Microtinae	12.6	35
Cricetinae	42.7	36
Gerbillinae	11.1	7
All others	1.6	0

Note. $\chi^2 = 16.37, p < .001$.
* $n = 68$ species.

Table 4
Comparison of Hystricomorphs With All Nonhystricomorph Rodents

Rodent	% with postpartum and lactational estrus		
	Families	Genera	Species
Hystricomorph	35	16	7
Nonhystricomorph	56	21	8

lacking delayed implantation, was also relatively common. No species achieved litter overlap exclusively by lactational mating (i.e., no phenotypes E and F were found).

One of the two examples of phenotype C can only equivocally be said to have delayed implantation. In *Microtus agrestis* mating can occur throughout lactation, beginning at postpartum. In a series of lactational matings in this species, Breed (1969) found an increase in gestation length when young were suckled simultaneously. Although statistically significant, this increase was small (0.24 day per additional pup) and may be of marginal biological significance.

Only three phenotype G species (with obligate cycling estrus) have been found: *Mesocricetus auratus* (Greenwald, 1967, and references therein), *Aplodontia rufa* (Pfeiffer, 1958), and *Sciurus carolinensis* (Deanesly & Parkes, 1933). Though other phenotype G species probably exist, it was not possible to identify them with certainty from the literature.

Discussion

I have asked two questions regarding the evolutionary and ecological context of PPE and LE, using a data base derived from the literature. First, is their phyletic distribution statistically nonrandom across taxa? Second, how do PPE, LE, and delayed implantation covary across species?

Postpartum estrus and lactational estrus were found to be phyletically widespread, and together they varied significantly in their prevalence among rodent families and subfamilies. There was also an association between these traits and reproductive rates at the family level. When these results are compared with previous characterizations of reproductive parameters, it appears that families with high intrinsic rates of increase tended to have a greater proportion of species with PPE and LE than more slowly

Table 5
Rodent Breeding Phenotypes

Phenotype	PPE	LE	DI	Frequency	Species
A	+	-	+	9	<i>Onychomys leucogaster</i> , <i>Peromyscus leucopus</i> , <i>Meriones unguiculatus</i> , <i>Tatera indica</i> , <i>Hydromys chrysogaster</i> , <i>Mus musculus</i> , <i>Pseudomys novaehollandiae</i> , <i>Rattus assimilis</i> , <i>R. norvegicus</i>
B	+	-	-	4	<i>Neotoma cinerea</i> , <i>Microtus oregoni</i> , <i>M. pennsylvanicus</i> , <i>Mesembriomys gouldii</i> ,
C	+	+	+	2	<i>Notomy alexis</i> , <i>Microtus agrestis</i> *
D	+	+	-	4	<i>Cavia aperea</i> , <i>Microtus ochrogaster</i> , <i>Myoprocta pratti</i> , <i>Grammomys surdaster</i>
E	-	+	-	0	
F	-	+	+	0	
G	-	-	(^b)	3	<i>Mesocricetus auratus</i> , <i>Aplodontia rufa</i> , <i>Sciurus carolinensis</i>

Note Exemplar species for phenotypes A-F were taken from Table 1 only when the presence (+) or absence (-) of postpartum estrus (PPE), lactational estrus (LE), and delayed implantation (DI) were known. Phenotype G species are taken from the text.

* The delay of implantation in this species, though statistically significant, is very small.

^b Delayed implantation is not in question when a species lacks both PPE and LE.

reproducing ones. These traits were significantly overrepresented in the Cricetidae, particularly in the subfamily Microtinae (the voles and lemmings). Microtine species have a greater reproductive capacity than other rodents, and females allocate a greater proportion of their total energy budget to reproduction (French, Stoddart, & Bobek, 1975; Millar, 1977). PPE and LE were significantly underrepresented in the Heteromyidae (kangaroo rats and pocket mice), a less fecund family adapted to arid habitats (Eisenberg, 1981; Eisenberg & Isaac, 1963; French et al., 1975; Millar 1977), and in the squirrel family Sciuridae, which reproduces at a low rate relative to other rodents (French et al., 1975). Further, litter overlap was found only in arboreal squirrels. This may imply that there are differences in female reproductive effort associated with arboreality.

Because PPE and LE were associated with high reproductive rates, it might be expected that they would be less prevalent among hystricomorph rodents. Species in this suborder have low reproductive rates and are characterized by long life spans, long gestations, and the production of a few large and precocial young (Eisenberg, 1981; Weir, 1974). However, the hystricomorphs were similar to nonhystricomorphs in prev-

alence of PPE and LE at the species, genus, and family level.

Adaptive explanation for PPE and LE may have to be sought below the family level, because the three traits surveyed can vary between closely related species (Table 1). Delayed implantation in particular is not a strongly conserved trait: Within a genus it may be present in one species and absent in another (e.g., within *Onychomys*, *Microtus*, and *Scotinomys*).

The degree to which PPE or LE constitutes a rapid breeding tactic depends on the degree of overlap between litters, a parameter that varies according to species-typical lengths of gestation and lactation. Many species are seasonally polyestrous, with a long breeding season relative to the conception-to-weaning interval. For such species litter overlap may represent a reproductive "high gear" during favorable times. Seasonally monestrous species may already be investing as much reproductive effort as they can.

The focus of this study is on the capacity of a species to breed by PPE or LE; however, the number of females breeding this way in a given population may vary according to seasonal factors. This proportion has been estimated for several wild populations, although diagnostic techniques used in the

field probably underestimate the incidence of lactational pregnancies (Greenwald, 1957; Perry, 1945). These studies show that the prevalence of overlapped breeding can vary greatly between and within breeding seasons. In a population of *Dipodomys merriami* studied for 32 months in Las Vegas, Nevada, 29% of the breeding females had overlapped litters (Bradley & Mauer, 1971). The proportion of adult *Lemmus trimucronatus* females breeding this way ranged from 0% to 70% per month during a 4-year study at Barrow, Alaska (Mullen, 1968). A 2-year study of *Microtus californicus* in San Francisco, California, found that overlapped breeding was absent in the first year but "widespread" in the second (Greenwald, 1957). Approximately 50% of pregnant adult *Rattus norvegicus* were also lactating in a 1-year study in Baltimore, Maryland (D. Davis & Hall, 1951). Only 1.7% of adult female *Tachyoryctes splendens* bred by litter overlap in a population studied for 2 years in Nairobi, Kenya (Jarvis, 1973). In a 2-year study of *Tamiasciurus hudsonicus* on Vancouver Island, British Columbia, there was no overlapped breeding in the first year, but all yearling and adult females bred this way in the second (Millar, 1970). A 3-year study of three populations of *Peromyscus maniculatus borealis* in the Kananaskis Valley, Alberta, found that 50%–100% of breeding females had two or more litters per season (Millar & Innes, 1983). Of these multiply breeding females, 82% bred by litter overlap. Finally, a 10-year study of *Thomomys bottae navus* in Davis, California, found overlapped breeding in the short, but not in the long, breeding peaks (Miller, 1946).

Postpartum estrus, lactational estrus, and delayed implantation were found in a variety of phenotypic combinations (Table 5). Although the familiar phenotype of *R. norvegicus* (PPE and LE with delayed implantation) was the most frequently seen, the literature survey documented three other phenotypes with litter overlap, results indicating a diversity of physiological traits underlying a common functional effect (reduced interlitter spacing). Equally interesting was the failure to discover the possible phenotypes E and F, that is, no species was found that lacks PPE and yet

mates at LE. This indicates that PPE is either phylogenetically more primitive or more easily evolved than LE.

Another finding was that no species followed LE with an appreciable delay of implantation. This result can be understood if one provisionally assumes that each trait independently functions to reduce litter overlap. A female can achieve maximal litter overlap by mating at PPE. She can achieve less overlap by (a) mating at PPE and delaying implantation or (b) mating at LE. Because LE and delayed implantation independently result in an interbirth interval longer than that of PPE, their co-occurrence would be functionally redundant; one would not expect to see delayed implantation following LE.

A selective advantage for litter-overlap breeding has been widely presumed (Conaway, 1968, 1971; Weir & Rowlands, 1973). However, the present results suggest that litter overlap may not be ubiquitous and that its selective advantage may be limited to certain taxa. One might ask: What limits its distribution? Several hypotheses deserve attention. I briefly consider estrus characteristics, reproductive energetics, and behavioral competition.

The endocrine physiology of PPE and LE may differ from CE (Hardy, 1970). The copulatory stimulation required for the induction of pregnancy varies between PPE and CE, though not consistently from species to species (Dewsbury, 1979a, 1979b; Dewsbury et al., 1979). Postpartum heat is shorter than cycling heat in some species (Blandau & Soderwall, 1941; Happold, 1976b; Lee & Horvath, 1969; Meyer & Meyer, 1944; Rowlands, 1949), while the pace of postpartum mating appears to be slower in others (Lanier & Dewsbury, 1977). The high intromission frequency seen in the first postpartum ejaculatory series in *Rattus norvegicus* (Gilbert, Pelchat, & Adler, 1980, in press) and *R. rattus* (Bean & Estep, 1981) may be characteristic of that heat. In addition, there is less fluid in the uterus during PPE than during CE in *R. norvegicus* (personal observations, 1980). Bronson, Dagg, and Snell (1968) reported the same for *Mus musculus*, although incorrectly citing an article by Merton. Whether these parameters have func-

tional significance for fecundity is an open question.

Do reproductive energetics limit a female's ability to carry off simultaneous gestation and lactation, as suggested by Daly (1979), Gustafsson et al. (1980), and others? In rodents, the female's energetic requirements increase slightly during gestation and far more substantially during lactation (Havera, 1979; Kaczmarski, 1966; Lochmiller, Whelan, & Kirkpatrick, 1982; Migula, 1969; Millar, 1975, 1979; Myrcha, Ryszkowski, & Walkowa, 1969; Randolph, Randolph, Mattingly, & Foster, 1977; Stebbins, 1977; Wang, 1925). By extrapolation it appears that the additional costs of gestation during lactation are marginal. This inference is supported by a study (Woodside, Wilson, Chee, & Leon, 1981) that found no difference in food intake between lactating rats and those that were lactating and pregnant.

As pointed out earlier, estrus occurs in many life-history contexts other than cycling virgin estrus. These contexts may involve complex interactions with other behavioral systems. The female in PPE or LE is not only primed to behave sexually, she is also physiologically prepared to behave maternally (Rosenblatt, 1965, 1975). This has fundamental implications for the organization of reproductive behavior, because the hormonal milieu and behavioral repertoires of copulation and maternity are often at odds. How is the potential conflict between these reproductive systems avoided? Observations on Norway rats mating at PPE indicate that females alternate between mating and maternal behavior, doing the latter almost exclusively during pauses (postejaculatory intervals) in the copulatory sequence (Gilbert et al., 1980, in press). This pattern of behavioral switching, known as "time-sharing" (McFarland, 1974), may be an adaptive solution to potential motivational conflict.

Interactions between temporally overlapped sibling litters may affect female reproductive success. Successive litters cohabit the maternal burrow in many species (Baker & Meester, 1977; R. Green, 1968; Olsen, 1982; also see references in Gilbert, Burgoon, Sullivan, & Adler, 1983). This could lead to direct competition (aggression)

or indirect competition for limited resources (nipples and milk) and might have a detrimental effect on the survival of the young (Hill, 1972; Rood & Weir, 1970; Weir & Rowlands, 1973). It could also lead to the evolution of interlitter cooperation, similar to the avian helpers at the nest phenomenon.

In summary, it appears that the prevalence of PPE and LE in rodents reflects trends in female reproductive effort at the family and subfamily level. In the future, it may be possible to create a more precise index of reproductive effort by using a measure of relative litter overlap: More extensive overlap might indicate greater reproductive effort. The relative extent of gestation/lactation overlap is a function of species-typical gestation and lactation length, and mode of estrus. These quantities are known for many species.

The present analysis suggests two areas for further investigation by physiological and comparative psychologists: (a) We need an evolutionary account of the phenotypic diversity underlying PPE, LE, and delayed implantation, and (b) we need to know more about the behavior and energetics of temporally overlapped litters, given the potential for cooperative and competitive interactions between them.

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