Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*

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Male-biased sexual dimorphism in both size and body mass is a common characteristic of many polygynous mammals and is often attributed to sexual selection favoring large males. The degree of dimorphism is thought to be related to the potential for some males to monopolize access to estrous females, which is in turn related to the distribution of receptive females in space and time. In the present study, we investigated the relationship between the temporal distribution of breeding females and the degree of mass dimorphism among 11 populations of the common brushtail possum from northern Australia. Breeding patterns varied from complete aseasonality in some populations to a seasonal concentration of births within 2 or 3 months in others. We predicted that in populations in which mating opportunities were distributed throughout the year, dominant males would be able to monopolize access to larger numbers of estrous females than in populations in which matings were more seasonal, and in such populations, large body size in males would be favored. We found that dimorphism was related to seasonality of breeding, being greatest in populations with a more aseasonal pattern. Mean body mass of male possums also decreased with increasing population density. Population density may influence the degree of breeding synchrony within populations, particularly in locations with a more seasonal climate. The present study is the first to demonstrate plasticity in mass dimorphism in response to local variation in the synchrony of breeding in a mammal species. **Key words:** breeding seasonality, polygyny, population density, reproductive synchrony, sexual dimorphism, sexual selection. *Trichosurus vulpecula.* [Behav Ecol 14:818–822 (2003)]

Most mammals have a polygynous mating system, in which males compete for access to breeding females (Clutton-Brock, 1989; Krebs and Davis, 1981). Thus, sexual selection is expected to favor adaptations, such as large body size, that enhance reproductive success in males during combat (Clutton-Brock et al., 1979; Schulte-Hostedde et al., 2001; Trivers, 1972). However, the mating success of females is less dependent on body size, and females are likely to adopt a more conservative growth strategy and invest resources into the production and provisioning of offspring rather than into growth (Reeve and Fairbairn, 2001; Schulte-Hostedde et al., 2001; Trivers, 1972). Accordingly, the majority of mammals show male-biased sexual dimorphism, with adult males larger and/or heavier than adult females (Krebs and Davis, 1981; Weckerly, 1998). However, recent studies have also associated sexual dimorphism in mammals with population density (LeBlanc et al., 2001), diet quality and selection (Clutton-Brock et al., 1987; Perez-Barberia and Gordon, 1999), latitude and climatic variables (Quin et al., 1996; Storz et al., 2001), disease (Pontier et al., 1998), and habitat use (Clutton-Brock et al., 1977), in addition to reproductive strategy (McElligott et al., 2001).

When females show a seasonal breeding pattern, and where individuals are solitary and spatially dispersed, polygyny potential and variance in male reproductive success may be reduced (Emlen and Oring, 1977). Smaller males can exploit the fact that more competitive males are involved in consorting and mating with females elsewhere (Say et al., 2001). If large dominant males are unable to control access to large numbers of females, there will be less benefit to allocating energy into additional growth. Therefore, we can predict that levels of sexual dimorphism will be lower in populations with seasonal reproduction. Conversely, when breeding occurs continuously throughout the year, large dominant males may potentially sire a greater proportion of offspring (Say et al., 2001), and the degree of sexual dimorphism should be higher. Few studies have previously investigated the influence on mammalian male mating strategies of the distribution of receptive females in time, whereas a great deal of research effort has centered on the effects of the distribution of receptive females in space (for review, see Clutton-Brock, 1989). This may be because many of the most intensively studied mammals have highly seasonal breeding patterns and thus do not provide the variation in seasonality needed to reveal potential effects on reproductive strategies of males and sexual dimorphism. Thus, little is known of the extent to which differences in breeding seasonality between populations can influence the development of sexual dimorphism within a species.

Density-dependent factors may also exert an influence on breeding seasonality through their effect on breeding synchronization. Ims (1990) defines reproductive synchrony as "a phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone." Breeding synchrony can occur in populations that show breeding seasonality, resulting in a tighter clustering of births than climatic seasonality alone would predict (Ims, 1990). However, reproductive synchrony can also occur in the absence of breeding seasonality, in relatively aseasonal tropical regions, and a variety of studies have demonstrated...
that estrous synchronization between sexually mature females can be socially induced by external olfactory cues (see Ims, 1990; Johannesen et al., 2000). Therefore, if high population density results in increased contact between individuals, this may stimulate ovarian activity and synchronize estrus between females.

The common brushtail possum, *Trichosurus vulpecula*, is an ideal model animal with which to investigate the interactions between sexual dimorphism, breeding seasonality, and population density. Although possums have a predominantly polygynous mating system (Smith and Lee, 1984), the degree of polygyny varies considerably between populations (Day et al., 2000). Males often have overlapping home ranges and compete for access to estrous females; both males and females are generally solitary (Winter, 1976). In Australia, large dominant males reportedly consort with females for 30–40 days before mating (Winter, 1976), and this behavior could put a severe limit on the number of females any one male could mate with during a seasonal or synchronous breeding cycle. Population density and levels of sexual dimorphism are also variable among Australian populations (see below). Breeding seasonality is broadly related to latitude, with a short breeding peak during the early autumn characteristic of the temperate south, often with a smaller, more variable breeding peak in the early spring. The spring birth peak is often produced by females in good condition giving birth to a second young (Kerle, 1984). Year-round breeding is commonly found in the tropical north. This latitudinal pattern is thought to be owing to environmental cues, such as photoperiod, climatic variation, and food availability, influencing the onset of estrus (Kerle, 1984). However, in the tropical north of Australia, breeding season can range from highly seasonal to year-round over relatively small geographic distances, suggesting that breeding seasonality is not constrained by climatic seasonality alone and that other factors must contribute to the degree of breeding seasonality in these populations.

In this article, we use data from 11 possum populations located in the north of Australia to investigate how variation in breeding seasonality between populations influences sexual dimorphism. We also address the power of population density to influence sexual dimorphism, in respect to its potential effect on the ability of males to find multiple mates within their home range, its relationship with individual body mass of adult males and females, and its possible influence on breeding seasonality itself, through increasing estrous synchrony within a seasonal breeding pattern. We predict that seasonality of breeding will be negatively correlated to levels of male-biased sexual dimorphism and that increasing population densities may result in a higher level of reproductive synchrony within populations.

**METHODS**

Data were collected in our own field studies of five possum populations in the Mt. Fox region (18°50' S, 145°46' E), one population at Hervey Range (19°23' S, 145°26' E), and one population on Magnetic Island (19°10' S, 146°50' E), all located in North Queensland (Figure 1). Data from two other Magnetic Island sites were taken from a study by Pieters (1985). Further data were taken from studies conducted in Brisbane, Southern Queensland (27°32' S, 152°53' E; Winter, 1976) and Jabiluka in the Northern Territory (12°28' S, 132°15' E; Kerle, 1998; Kerle and Howe, 1992). Possums at each of our seven North Queensland sites were live-trapped by using wire mesh traps over a period of at least 12 months in order to determine the distribution of births throughout no less than one full breeding season. The five Mt. Fox populations were trapped on average four times per year, over a period of at least 3 years. Individual possums were not found to travel between any of the Mt. Fox populations over the period of the study; thus, they were considered to be five independent sites. The three Magnetic Island sites and the Hervey Range site were trapped once monthly for a period of 1 year. Each animal was also weighed, to the nearest 20 g, with a spring scale during each trapping session. Population size was calculated as the minimum number of animals known to be alive (Krebs, 1966), per hectare, determined from live-trapping data for all sites except Brisbane. For the Brisbane site, the number of animals known to be alive was estimated by a spotlighting transect method (Winter, 1976). The five Mt. Fox sites and the Hervey Range site were approximately 40 ha, the three Magnetic Island sites were approximately 10 ha., the Jabiluka site was approximately 5 ha, and the Brisbane site was 17 ha.

Breeding seasonality was determined by assigning a date of birth to all unweaned juveniles, defined as dependent pouch-young or young-on-back captured with their mothers during trapping sessions. Date of birth, in days, was estimated from head length by using growth equations specifically formulated for the North Queensland populations. For pouch young with a head length of less than 25 mm in length,

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\text{Age (in days)} = 2.95 \times \text{head length (in mm)} - 16.82
\]

For pouch young with a head length greater than 25 mm in length,

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\text{Age (in days)} = 2.95 \times \text{head length (in mm)} - 18.55
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The first measurement of head length, usually taken when the offspring was still pink and permanently attached to the teat, was used in the analysis, as the accuracy of these equations in aging pouch young has been found to decrease as offspring grow larger. Breeding seasonality was expressed as the percentage of births occurring in the peak 2 months, whether these months were consecutive or not, for each population. Populations with a more continuous, year-round breeding pattern therefore had a lower value of this index than did those with a pronounced seasonal breeding peak.
Breeding seasonality is expressed as the percentage of births occurring in the peak 2 months. Sexual dimorphism values are male body mass divided by female body mass (kg). MI indicates Magnetic Island site; MF, Mt. Fox site.

**RESULTS**

The distribution of births, levels of sexual dimorphism, and population density were found to vary considerably within the 11 populations (Table 1). None of the key variables were found to be significantly related to latitude (\( \delta \)) (breeding seasonality: \( F_{1,9} = 1.05, p = .33, R^2 = .11 \); sexual dimorphism: \( F_{1,9} = 0.03, p = .57, R^2 = .004 \); population density: \( F_{1,9} = 0.04, p = .83, R^2 = .005 \)), mean annual rainfall (mm) (breeding seasonality: \( F_{1,9} = 3.25, p = .12, R^2 = .35 \); sexual dimorphism: \( F_{1,9} = 0.43, p = .55, R^2 = .07 \); population density: \( F_{1,9} = 1.84, p = .22, R^2 = .23 \)), or mean maximum temperature (\( ^\circ C \)) (breeding seasonality: \( F_{1,9} = 1.39, p = .29, R^2 = .18 \); sexual dimorphism: \( F_{1,9} = 0.06, p = .80, R^2 = .01 \); population density: \( F_{1,9} = 1.11, p = .33, R^2 = .16 \)).

The level of male-biased sexual dimorphism within possum populations was significantly related to breeding seasonality (\( F_{1,9} = 16.64, p = .002, R^2 = .65 \)) (Figure 2). Populations with a more continuous breeding season had a greater degree of sexual dimorphism than did those with a short seasonal peak. A standard least-squares multiple regression determined that there was no significant interactive effect of population density and breeding seasonality on sexual dimorphism (\( F_{1,9} = 0.15; p = .7 \)) and no effect of population density on sexual dimorphism that was independent of the relationship between breeding seasonality and sexual dimorphism (\( F_{1,9} = 2.23; p = .17 \)).

There was a trend for an increase in breeding seasonality with increasing population density (\( F_{1,9} = 1.95, p = .19, R^2 = .18 \)). The Northern Territory population was found to be a significant outlier in this analysis by using the jackknife distance (Mahalanobis) method, and when this population was removed from the analysis, the relationship between reproductive seasonality and density became significant (Figure 3, \( F_{1,9} = 8.72, p = .02, R^2 = .52 \)). This population was not found to be a significant outlier in any of the other analyses. An increase in population density also resulted in a decrease in the mean male body mass (\( F_{1,9} = 5.55, p = .04, R^2 = .38 \)); however, no such relationship was found between density and female body mass (\( F_{1,9} = 3.01, p = .11, R^2 = .25 \)).

**DISCUSSION**

Sexual dimorphism and breeding seasonality

Our data support the prediction that male-biased sexual dimorphism in brushtail possums is significantly more pronounced in populations with a more continuous breeding pattern. Substantial differences in sexual dimorphism and seasonality were observed between populations that were geographically very close to one another, and the results confirm that these differences were not the result of latitudinal or climatic effects. According to the sexual selection hypothesis of sexual dimorphism, levels of male-biased dimorphism...
in mammals should be correlated to the degree of polygyny within a population (Boonstra et al., 1993). Asynchrony of breeding can influence the operational sex ratio of a population by increasing the number of receptive females per male, resulting in greater polygyny potential (Emlen and Oring, 1977). Say et al. (2001) recently investigated the effects of reproductive synchrony on the degree of polygyny in the domestic cat (Felis catus) and found that variance in male reproductive success was four times greater in years in which females bred asynchronously, compared with years in which females bred synchronously. To our knowledge, the present study is the first on a mammal to clearly correlate levels of reproductive synchrony on the degree of polygyny in the domestic cat (Felis catus) and found that variance in male reproductive success was four times greater in years in which females bred asynchronously, compared with years in which females bred synchronously. To our knowledge, the present study is the first on a mammal to clearly correlate levels of sexual dimorphism with variation in breeding seasonality among populations. However, the results do concur with those of a recent study on a socially monogamous seabird, the brown booby (Sula leucogaster, Tershy and Croll, 2000), in which it was found that males showed a significantly greater degree of sexually dimorphic plumage in populations in which birds bred year-round. However, in populations in which breeding occurred within a short 90-day period, there was little male sexual dimorphism in plumage (Tershy and Croll, 2000). The investigators suggest that further data will reveal that breeding synchrony prohibits sequential polygyny, resulting in reduced male-male competition and a consequent decrease in the need for sexually dimorphic traits (Tershy and Croll, 2000).

Population density and breeding seasonality

The data also indicate that population density influences breeding seasonality. This may suggest that high population density results in an increase in reproductive synchrony among females, within a seasonal breeding pattern. In the North Queensland study areas, the possum populations are from a relatively small geographical area, and variations in seasonality were not explained by differences in climatic seasonality or latitude. Density in these populations is primarily related to soil fertility (Johnson et al., 2001). In seasonal environments, breeding is usually restricted to the part of the year when resources are most abundant (Bronson, 1989). Kerle and Howe (1992) have suggested that the continuous breeding cycle of possums in the Northern Territory can be directly related to their tropical environment, where there are no annual periods of food shortage, allowing year-round breeding regardless of population density. This may, in part, explain why the Northern Territory population was found to be a significant outlier in our analysis. However, breeding synchrony has also been observed in tropical aseasonal regions and has been linked to a number of ecological and sociobiological processes (for review, see Ims, 1990). Research has shown that pheromonal signals, often secreted in urine, from individuals of the same species can stimulate ovarian activity and synchronize estrus within a population (for review, see Rekrotz et al., 2001). Furthermore, a recent study found that the presence of males significantly increased the incidence of ovulation in female brushtail possums, after the removal of pouch young (Crawford et al., 1998). If high density results in increased exposure to such signals, either from males and/or other females, the breeding cycles of individual females are more likely to be entrained with their neighbors (Johannesen et al., 2000), possibly resulting in population-wide breeding synchrony.

Our results also suggest that population density may affect the individual body mass of adult male possums. Similar relationships have also been found in ungulates such as bighorn sheep (Ovis canadensis, LeBlanc et al., 2001), roe deer (Capreolus capreolus, Vincent et al., 1995), and red deer (Cervus elaphus, Clutton-Brock et al., 1982), in which results indicated that body growth of males was limited by resource availability at high density. In bighorn sheep and roe deer, it was also suggested that females were able to undergo compensatory growth later in life, resulting in a lower degree of sexual dimorphism (LeBlanc et al., 2001; Vincent et al., 1995). This explanation could also be highly applicable to possums, which consume a low-quality, high-biomass diet comparable to that of ungulates (Nugent et al., 2000) and is supported by the fact that our results found no relationship between density and a decrease in female body mass.

In conclusion, our study provides evidence that breeding seasonality can influence patterns of sexual dimorphism in brushtail possums. This result implies that aspects of the reproductive behavior of males, and patterns of male-male contact, will also vary substantially between populations. Recent studies on the mating system of T. vulpecula have...
found inconsistent results; Taylor et al. (2000) found no relationship between male age or mass on mating success in T. vulpecula in New Zealand farmland, whereas Clinchy (1999) found a clear positive association between male body mass and mating success in possums in old-growth Eucalyptus forest in southern Australia, suggesting a more polygamous mating system. On-going paternity analysis of our seven Queensland populations will clarify the relationship between breeding seasonality, mass dimorphism, and variance in male reproductive success.

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