Sexual selection and mating system in *Zorotypus gurneyi* Choe (Insecta: Zoraptera)

I. Dominance hierarchy and mating success

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Summary. Social behavior of a species in the little-known insect order Zoraptera is described for the first time. *Zorotypus gurneyi* Choe (Insecta: Zoraptera) is a wing-dimorphic species that lives colonially under the bark of rotting logs in central Panama. Males are larger than females in total body size and fight each other to gain access to females. Highly linear and stable dominance hierarchies exist among males. Higher-ranking males show such agonistic behavior as jerking, chasing, head-butting, hindleg-kicking, and grappling, whereas subordinates often try to avoid contacts. Higher-ranking males, the dominant males in particular, are well recognized by others and relatively free of injuries. Although the dominant males are often the largest, the correlation between body size and dominance rank is not always significant. The mating system of *Z. gurneyi* is an example of female defense polygyny in which the dominant males obtain the majority of matings (75% on average). Mating success among *Z. gurneyi* males is much more variable than that of some lekking species.

Key words: Dominance – Female defense polygyny – Lek – Mating success – Zoraptera – *Zorotypus gurneyi*

Introduction

Sexual selection has two components: intrasexual and intersexual selection (Darwin 1871). Primarily because females invest more in offspring than males, males typically compete for females (*intrasexual selection*) and females exercise a choice of mates (*intersexual selection*) (Bateman 1948; Trivers 1972; Bateson 1983). Males adopt various mating strategies to influence female mate choice (Alcock 1979; Rubenstein 1980; Austad 1984). Dominance relations among males predetermine their mating success to a large extent in some group-living species

such as elephant seals (LeBoeuf 1974), red deer (Clutton-Brock et al. 1982), and yellow-rumped caciques (Robinson 1986). In olive baboons, however, male dominance rank is sometimes inversely correlated with consort success (DeVore 1965; Strum 1982).

Few insects have been studied with regard to the relationship between dominance hierarchy among males and their reproductive success (but see Breed et al. 1980; Crespi 1988). The zorapterans are colonial insects that live under the bark of rotting logs in tropical forests. Previously their biology was poorly understood, partly due to the difficulty of finding individuals in the field and maintaining healthy laboratory colonies. I developed a successful rearing technique which permits behavioral experiments on these little-known insects (Choe 1990, 1992). This paper provides the first information on the social behavior of the order Zoraptera and describes in detail (1) the social structure, (2) social behavior and dominance relationships among males, and (3) effects of social dominance on mating system and reproductive success in *Zorotypus gurneyi* from the lowland forests of central Panama.

Methods

Collecting. The study colonies of *Z. gurneyi* were collected from Parque Nacional Soberania, adjacent to the Panama Canal in central Panama, from November 1986 to March 1987. Decaying logs were located along a dirt road ("Pipeline Road") that starts from Gamboa and transverses the park. The bark was peeled off little by little and zorapterans were gently swept into a collecting jar by a fine brush. Every effort was made to ensure that the entire colony

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was recovered. Any incompletely collected colonies were not used in this study. Additional information on collecting zorapterans is provided in Choe (1992).

Identification of individuals. Individual zorapterans were identified by several natural features that vary among individuals, such as the number of antennal segments on each side, missing legs, and attachment pattern of mites. Although normal *Z. gurneyi* individuals have nine segments on each antenna, some are born with unequal numbers of antennal segments. Zorapterans also lose antennal segments from fighting. The combination of the two numbers, e.g., '8-9' to indicate an individual with eight segments on the left antenna and nine on the right, was surprisingly effective in distinguishing individuals. Deutonymphs of an unidentified species of mite (*Histiostoma* sp. nov.; B. M. OConnor, personal communication) were found attached to various body parts of *Z. gurneyi*. A number of *Histiostoma* species are known to be phoretic on insects (OConnor 1993). Interestingly, the attachment sites of mites never changed during the experimental period and thus proved to be an effective additional identification mark. Only when these natural marks failed to provide adequate means of identification were individuals marked with a dot of white paint on one of the thoracic tergites. Only three males in colony VI were marked and no obvious abnormal behavior was noticed from these males.

Observation. Although colonies of various sizes were collected, colonies with fewer than six males were excluded from the study because a highly linear hierarchy among five or fewer individuals can be obtained by chance when the actual dominance relationships are random (Appleby 1983). Nonetheless, a few small colonies with fewer than six males were also observed, although the data from such colonies were not included in the quantitative analysis. General patterns in intermale interactions and mating system were similar to those from the study colonies. Colonies with ten or more males were also excluded, because it was increasingly difficult to record all behavioral interactions. The median number of males in all field-collected colonies (*n* = 39) was five.

Each colony was reared separately in the Smithsonian Tropical Research Institute laboratory on Barro Colorado Island in Panama. Plaster of paris was mixed with water and poured into a 14-cm diameter petri dish. Once the plaster had hardened, the center (approximately 12 cm diameter, 0.5 cm deep) was carved out. The carved-out area or 'arena' was covered with red plastic to reduce disturbance from air turbulence and light. The zorapterans were kept in darkness with debris from their own natural habitat. They were fed yeast and crushed laboratory-rat chow, and humidity was maintained by sprinkling water on the uncarved portion of plaster along the rim of the petri dish. Observations were made under a dissecting microscope using a fiber-optic light source. Most individuals were eyeless and appeared to behave normally under cold light.

Observations began within 1 or 2 days after each colony was housed in the laboratory. Each colony was observed for 60 h (360 h for six colonies) during 5–7 consecutive days. In artificially constructed colonies, over 90% of all matings occurred within the first 4 days after the colonies were formed (Choe 1990). Observation sessions were arranged during both day and night to cover at least two full daily cycles for each colony. No marked difference was noted between the daily and nightly observations.

To determine dominance relationships among males, the following five types of behavioral interactions were recorded in terms of frequency, duration, win/loss, and injury:

– *Contact avoidance.* When two males are within one body-length of each other, they vibrate their antennae rhythmically and one walks away before touching the other.
– *Chasing.* One male runs after the other. It often follows other types of behavioral interaction such as head-butting or hindleg-kicking.
– *Head-butting.* After a brief antennation, one male pushes the other with his head.

– *Hindleg-kicking.* Upon encountering another male, a male often turns around and immediately raises his hindquater. After a short pause, one male kicks the other with his hindlegs in much the same way that ungulates do. The male being kicked usually kicks back in response.
– *Grappling.* Two males grab each other and roll around together. It is the most escalated form of intermale aggression, through which males often lose such body parts as antennal segments and/or hindlegs.

After observation, all adults were killed in 75% alcohol, and their body lengths and hindfemur lengths were measured to the nearest 0.01 mm with an ocular micrometer. Voucher specimens have been deposited in the Museum of Comparative Zoology, Harvard University.

Analysis. Based on the outcomes of agonistic interactions among males, a dominance matrix was derived for each colony, using the method provided by Brown (1975). All six matrices were then combined to show mean scores. Males ranked below six were pooled and as a result there were six males in each of seven rank catergories.

The linearity of the dominance hierarchy among males in each colony was estimated using Landau's index of linearity (*h*) (Landau 1951):

$$h = 12/(N^3 - N) \Sigma [S_i - (N-1)/2]^2$$

N is the total number of males in a colony and S_i is the number of individuals subordinate to *i*. The index value generally ranges from 0 (absence of linearity) to 1 (perfect linearity) and its statistical significance can be estimated using the method described by Appleby (1983).

The degree of mating skewness was determined by using the index, *H*, proposed by Bradbury et al. (1985):

$$H = N/(N-1) \Sigma (C_i - 1/N)^2$$

where *N* is the number of males in a colony and C_i is the proportion of matings attributed to the *i*th male. The value of *H* varies from 0 (perfectly even distribution of matings) to 1 (total monopoly by a single male).

Non-parametric tests were used whenever the assumptions of normality were not met. All tests are two-tailed and data are presented as mean ±1 SD.

Results

Colony composition

In the six study colonies females were generally more abundant ($\bar{x} \pm SD$ = 10.5±4.1) than males (7.0±1.3) (Table 1). Each colony had, on average, 12.8±1.9 nymphs at various developmental stages (Table 1). Four nymphs emerged as adults (3 males and 1 female) during the observation period and they are treated as adults in Table 1. Winged individuals were extremely rare. All five winged adults were female. The average colony size was 30.3±5.4.

Size distribution

Males have longer hindfemora (0.79±0.03 mm, *n* = 42) than females do (0.73±0.02 mm, *n* = 63; Mann-Whitney *U*-test, *Z* = 7.318, *P*<0.001) (Fig. 1). There are 9–11

Table 1. Composition of six *Zorotypus gurneyi* colonies used in the study

Colony	Adult male	Adult female	Nymph	Total
I	6	8	13	27
II	6	4	11	21
III	6	15	11	32
IV	7	10	16	33
V	8	14	14	36
VI	9	12	12	33
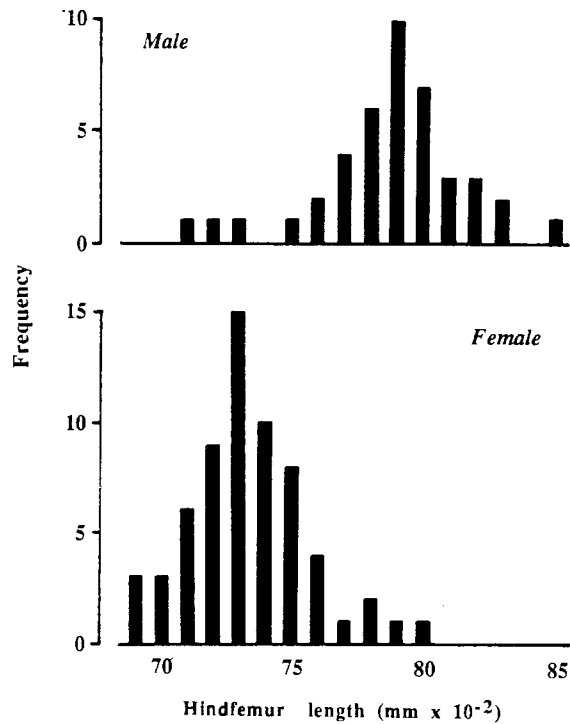
Fig. 1. Size (hindfemur length) distributions for males ($n = 42$) and females ($n = 63$) of *Zorotypus gurneyi* in six study colonies

thick spines on the posterior margin of each hindfemur in both sexes. Females have smaller spines as they have smaller hindfemora. There was a significant positive correlation between the total body length and hindfemur length ($r = 0.866$, $P < 0.001$, $n = 105$), indicating that hindfemur length is a good indicator of body size.

Agonistic interactions and dominance hierarchy

As mentioned above, *Z. gurneyi* live in darkness under the bark of rotting logs, and most individuals are wingless and eyeless. Antennation appears to be the major mode of communication. After a single stroke of antennation, individuals appear able to assess one another with respect to relative dominance and sex.

A total of 16,252 male-male interactions were recorded from six study colonies. The most common interaction was *contact avoidance* (43.8%; 7112), closely followed by *head-butting* (40.8%; 6634). Males chased others 2431 times (15.0%) and each chase usually took less than a second. Nearly half (48.6%) of all recorded chases were done by the dominant males. In fact, chasing was the most common (67.7%) behavior of the dominant males. Although males were engaged in a rear-to-rear hindleg-raising display 184 times, they kicked with the hindlegs only 72 times (0.4%). Only three grapple fights were observed and they lasted for less than 1 s. Grappling zorapterans grabbed each other's body parts in much the same way that professional wrestlers perform arm-locks; hindfemoral spines were used to pin down and pull the opponent's antenna, leg, or even head.

I considered the male that walked away or fled in any of the four types of behavioral interaction the loser and the compiled dominance matrix is given in Table 2. From these win/loss data emerged two categories of males: higher-ranking males, i.e., the first, second, and third-ranking males whose win/loss ratios were 80% or higher, and lower-ranking males whose win/loss ratios were 20% or lower. The dominant males had fewer interactions than the second-ranking males in all six colonies ($\chi^2 = 17.71$, $P < 0.01$), because most subordinates stayed away from the dominant males.

Hierarchies of five out of six colonies had linearity indices greater than 0.9 (Table 3), which is considered highly linear (Chase 1974; Bekoff 1977) and all were significant ($P < 0.01$), indicating that dominance relationships were not generated randomly in all six colonies. Another commonly used measure of linearity, Kendall's coefficient (Appleby 1983), was also estimated and the values were virtually identical to those of Landau's index. In only 933 interactions (5.7%) did a higher-ranking male lose to a lower-ranking male (Table 2), indicating that dominance relationships among males were clear in most cases.

Table 2. Outcome of agonistic interactions among *Zorotypus gurneyi* males

Rank	1	2	3	4	5	6	>6	Wins
1	—	234±86	214±92	176±53	99±22	60±10	38±5	801±235
2	0	—	356±94	301±79	228±28	110±17	91±5	1040±244
3	0	1±1	—	212±30	163±31	90±32	63±5	497±98
4	0	1±1	15±5	—	81±13	44±15	39±9	159±31
5	0	0	9±3	53±15	—	41±14	31±8	119±19
6	0	0	0	22±11	31±11	—	30±11	68±28
>6	0	0	0	12±2	12±2	25±6	—	49±8
Losses	0	235±87	593±107	770±81	608±43	356±65	293±14	2709±349

Each figure is mean ± SD estimated from six study colonies

Table 3. Landau's index (h) of linearity of dominance hierarchies and values of Spearman's correlation (r_s) between hindfemur length and dominance rank among *Zorotypus gurneyi* males in six study colonies

Colony	h	Significance	r_s	Significance
I	1.000	$P<0.01$	0.943	$P<0.05$
II	1.000	$P<0.01$	1.000	$P<0.005$
III	1.000	$P<0.01$	0.405	ns
IV	1.000	$P<0.01$	0.893	$P<0.05$
V	0.833	$P<0.01$	0.405	ns
VI	0.967	$P<0.01$	0.683	ns

Table 4. Frequency of injuries among *Zorotypus gurneyi* males in each dominance rank

	Dominance rank						
	Higher-ranks			Lower-ranks			
	1	2	3	4	5	6	>6
Missing antennal segments	1	2	3	3	5	2	4
Missing a hindleg	0	0	1	2	3	2	2

The dominant male behaved in an obvious way. He walked slowly in the center of the arena, often vibrating his antennae vigorously in a rhythmic fashion, whereas subordinates walked swiftly along the edge of the arena (Fig. 2). Only the second, the third, and occasionally the fourth highest males sometimes ventured near the dominant male. The dominant male also showed frequent jerking movements, most of which were not necessarily aimed at any particular individual. The duration of a jerking bout lasted for 4.2 ± 6.6 s ($n = 40$). All three cases of grapple fights were initiated by the dominant males.

The dominant male was also the largest in four colonies; in the other two the second and third largest male, respectively, were dominant. In general, there was a trend for higher-ranking males to be larger, but dominance rank and hindfemur length were not significantly correlated ($P>0.05$) in three out of six colonies (Table 3). Higher-ranking males generally had darker exoskeletons than lower-ranking males, suggesting that age might be an important determinant of dominance.

Among the most noticeable injuries were losses of antennal segments and a hindleg. Frequency of missing antennal segments did not significantly differ between higher-ranking and lower-ranking males ($\chi^2 = 1.35$, $P>0.05$), while missing a hindleg was much more frequent among lower-ranking males than higher-ranking ones ($\chi^2 = 4.41$, $P<0.05$; Table 4). Individuals were missing up to six segments in either antenna, but none were missing both hindlegs. Although few injuries were witnessed at the point of infliction, I observed two subordinate males lose five antennal segments and a hindleg, respectively, during grapple fights with the dominant males.
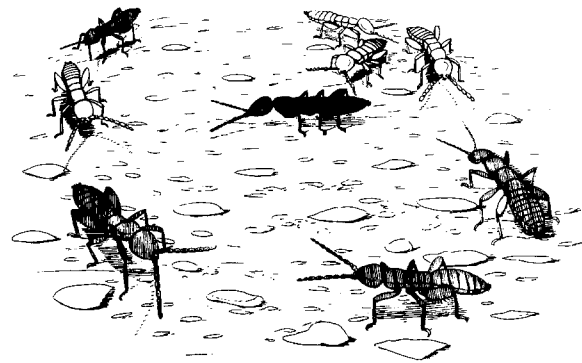

Fig. 2. A typical scene in a *Z. gurneyi* colony, showing the dominant male (*black*) in the center, subordinate males (*shaded*), and females (*white*)

Behavior of females

Females were constantly pursued by males. They also showed hindleg raising and kicking behavior toward males and sometimes females. Females tended to form a loose but definite clump and the dominant male appeared to defend the harem by constantly chasing subordinates away from it (Fig. 2).

Behavior of nymphs

Nymphs' behavior was essentially unaffected by the dominance hierarchy. Most spent much of their time hiding in crevices. However, when they move about, they ran into and disturbed any member of the colony. Adults of either sex appeared to provide parental care for nymphs. No care or cannibalism was observed of eggs.

Dominance and mating success

The dominant males constantly chased and attempted to copulate with females. Precopulatory behavior was rather simple and brief. Following a brief antennation and jerking by the male, some females turned around and took a few steps backward toward the male. The male then almost instantaneously turned around and copulated with the female, turning upside down as he did so (Fig. 3). Copulations lasted for 55.6 ± 4.9 min ($n = 76$). The durations of copulation by the dominant and subordinate males did not differ ($P>0.05$; Mann-Whitney U-test). Copulating pairs were often attacked by others, most of whom were female (86.2%). The copulating female either fought back or ran away dragging the male around. It appeared that the male terminated a copulation by releasing the female.

Of 76 copulations, 55 (72.4%) were performed by the dominant males (Fig. 4). On average the dominant male copulated 9.2 ± 2.9 times ($74.5 \pm 10.8\%$; $n = 6$ colonies), whereas subordinate males obtained only occasional copulations. The mean value of H (index of mating skew) for the six colonies was 0.510 ± 0.143 (range: 0.286–0.580).
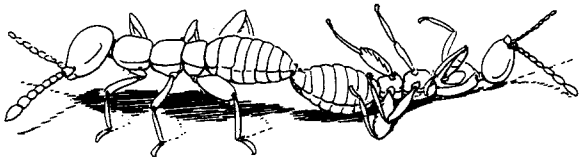
Fig. 3. Mating posture of *Z. gurneyi*: the *female* maintains a forward upright position, while the *male* is upside down
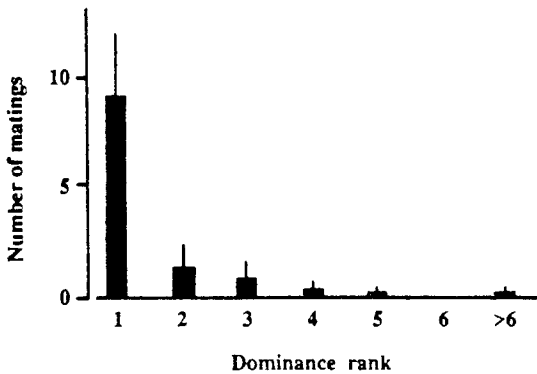

Fig. 4. Number of matings (mean ± SD) obtained by males of different dominance ranks in six study colonies. Each rank category has six males

A total of 48 females (76.2%) mated only once during the observation period. Eight females (12.7%) mated twice, while four (6.3%) mated three times. Of the 12 females who mated more than once 5 mated with more than one male. Three females (4.8%) were never seen mating.

Field observation

Field observations were made by replacing the bark with a red plastic sheet. Although detailed behavior of individuals could not be monitored, the general appearance of movements in the field colonies resembled that seen in the laboratory colonies. Occasionally, I encountered large colonies with up to several hundreds of individuals in the field. I could not determine whether a single most dominant male monopolized the access to most females or several males held harems of various sizes in such a large colony.

Discussion

Mating system

The mating system of *Z. gurneyi* may represent a form of female defense polygyny. Dominant males did not appear to defend resources or oviposition sites used by females. Instead, they directly pursued females. Females tended to form a loose but definite clump or harem. Dominant males appeared to actively prevent other males from gaining access to females in much the same way that stags do (Clutton-Brock et al. 1982).

The direct monopolization of a harem of females is rare in insects (Thornhill and Alcock 1983). Most insects are highly mobile and do not live in a closed social unit. In those cases where harem defense occurs, females usually emerge in clusters (see Thornhill and Alcock 1983 for examples). In *Z. gurneyi*, however, adult females emerge throughout the year, but live in more or less confined spaces. Insects that live in a closed microhabitat, such as the space under the bark, and/or have reduced flight abilities would be good candidates for the direct monopolization of females by males.

Intermale conflicts and dominance hierarchy

Since early study of social dominance in domestic chickens (Schjelderup-Ebbe 1922), dominance hierarchies have been thought to be highly linear in most species. According to an analysis by Jackson and Winnegrad (1988), however, only 26 (41.9%) out of 62 hierarchies reported in the literature were strongly linear.

Zorotypus gurneyi males establish and maintain highly linear dominance hierarchies. In this study, only colony V had a linearity index value below 0.9. The value of Spearman's correlation between body size and dominance rank for colony V was also insignificant, and the lowest among six colonies. In that colony the largest and second largest males were ranked sixth and fifth, respectively, and had injuries; possibly they were aging and descending the hierarchy. This transient situation may have been responsible for the lowest degree of mating skew recorded from this colony.

Dominance hierarchies among *Z. gurneyi* males were also stable as well as linear. None of the dominant males was displaced by other males during the observation period, although they were sometimes challenged by immediate subordinates. Dominance ranks were well recognized, especially for the top three males, as indicated by the order of magnitude differences between wins and losses. The exact mechanism of rank or individual recognition is unclear, but contact avoidance behavior among males suggests that some sort of short-range chemical signal may be involved in the communication system of *Z. gurneyi*. A brief antennation between individuals, often consisting of a single stroke, is perhaps a way of verifying chemically-transmitted information.

Because the study colonies were collected more or less intact in the field where the dominance hierarchies had already been established, it was not possible to witness how the hierarchies develop in *Z. gurneyi*. Rare glimpses were provided when three nymphs emerged as adult males during the observation period. The dominant males were always the first to approach and make a series of attacks toward newly emerged males. These newly emerged males tended to venture toward the center of the arena more often than other subordinate males, possibly provoking the dominant males, but the dominant males also appeared to actively seek out and chase the new males. Many of the males at the bottom of the hierarchies had a pale exoskeleton, indicating that they were young males. Adults emerge throughout the year and it appears

that newly emerged males must start from the bottom of the hierarchy (Choe 1994).

Lower-ranking males were missing a hindleg much more frequently than higher-ranking ones, while frequency of missing antennal segments did not differ significantly between the two categories of males. Although antennation appears to be an integral part of communication among zorapterans, losing some antennal segments may not greatly affect their dominance dynamics. It is not always clear whether the relation between dominance and injury level is causal, but on two occasions I observed males descending the hierarchy after the loss of a hindleg during grapple fights (Choe 1994). The current dominant males may simply be those that have managed to avoid serious injuries in the past. Dominant males showed nearly continuous jerking and chasing movements. Such behavior may be energetically costly, but can reduce the risk of being injured in actual fights. Body size seems to be an important variable in determining the dominance hierarchy among *Z. gurneyi* males, but is generally overriden by the effects of age, or more specifically, the male's tenure i.e., length of time the male has been in the colony (Choe 1994).

Mating success and sexual selection

Dominant males had disproportionately more access to females and thus obtained the majority of matings in *Z. gurneyi*. On the other hand, nearly all females were seen to mate at least once in 5–7 days of observation. Thus, the intensity of sexual selection is greater on males than on females in *Z. gurneyi*. In this study, reproductive success is measured as mating success, which is obviously the compound result of several selective episodes (Howard 1978; Arnold and Wade 1984). The variance in male reproductive success depends on two factors: the variance due to differences in fecundity among females and the variance in the number of females with which a male mates (Wade and Arnold 1980). It was not possible to monitor how many eggs each female *Z. gurneyi* laid, because there was no prefered oviposition site for any particular female. Although multiple mating by females was only moderate in *Z. gurneyi*, there still is a potential for sperm competition because some females mate with more than one male.

Male mating success is most variable in polygynous species (Wilson 1975; Emlen and Oring 1977), and is thought to be most skewed in lekking species (e.g., Payne 1984). Contrary to this prediction, the *H* values for the six study colonies of *Z. gurneyi* were considerably higher (0.510 ± 0.143; range: 0.286–0.667; $n = 6$) than the values for 11 studies of five lekking species (0.337 ± 0.113; range: 0.154–0.515; $n = 11$) in Bradbury et al. (1985). The linearity and stability of the dominance hierarchy in *Z. gurneyi* may enhance the degree of mating skew. A more fundamental problem exists, however, as to which males ought to be included in the analysis. To accurately assess the actual mating distribution in polygynous species, all mature males in the population, reproductively successful or not, should be included. Most studies of polygynous species do not provide accurate information on how many males are present without territories or harems (Searcy and Yasukawa 1983). Exclusion of such males can reduce the degree of mating skew, and without such information, it is difficult to test if mating success is indeed more variable in lekking species than other polygynous species.

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