

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

II. Determinants and dynamics of dominance

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Abstract. Body size is clearly an important factor influencing the outcome of agonistic contests, but is often weakly correlated with dominance ranks in *Zorotypus gurneyi* Choe (Insecta: Zoraptera). The study of the development and dynamics of dominance relations using artificially constructed colonies show that age, or tenure within the colony, is the prime determinant of dominance among males. Dominance hierarchies become relatively stable within 2 or 3 days and males that emerge later normally begin at the bottom of the hierarchy regardless of size. Males interact much more frequently when they are simultaneously introduced to each other than when they are allowed to emerge at different times. In the latter case, males that emerge late appear to recognize relative dominance of older males and avoid direct contests. Considering the high correlation between dominance rank and mating success, there is a strong selective advantage to males that emerge earlier and such pressure of sexual selection may be responsible for the difference in life history strategies between *Z. gurneyi* and its sympatric congener, *Z. barberi* Gurney, in central Panama.

Key words: Age – Dominance – Life-history strategy – Size – Zoraptera

Introduction

Dominance relations in group-living animals are influenced by a number of factors such as body size, age, sex, hormones, experience, territorial familiarity, dominance status of parents, and group size (Schein 1975; Wilson 1975; Frank 1986; Hand 1986). Among these factors size and age are probably the most obvious and frequently investigated. In insects alone, body size has been found to be well correlated with the ability to win agonistic confrontations in a number of species (e.g., Alcock 1979;

Borgia 1980; Eberhard 1979, 1980; Hughes and Hughes 1982; Johnson 1982; Thornhill 1984; Crespi 1986a, b, 1988; Michener 1990).

Age is also a good correlate of dominance in other insects such as cockroaches (Schal and Bell 1983), wasps (West-Eberhard 1969; Hughes and Strassmann 1988) and sweat bees (Michener 1990 and references therein). West-Eberhard (1969) found in some *Polistes* wasps that emergence order determines dominance relations among workers. Similarly, the sequence of arrival at nest-founding site is the most important variable for founding queens (West-Eberhard 1969). Hughes and Strassmann (1988) described age-based dominance hierarchies in *Polistes instabilis* in which old workers are dominant even though they are often smaller than their younger subordinates. Schal and Bell (1983) also found that age rather than size predicts the outcome of intermale contests in *Nauphoeta cinerea*.

A recent study on dominance relations among males of *Zorotypus gurneyi* revealed that the correlation between body size and dominance rank is not always significant (Choe 1994). Although body size is clearly an important factor in determining the outcome of staged contests, it is significantly correlated with dominance rank in only half of the study colonies collected in the field (Choe 1994). Chase (1982, 1985) suggests that the discrepancies between observed and predicted dominance ranks based on individual characteristics such as size and age can be better understood by looking at the ontogeny of dominance relations. This study investigates relative importance of size and age on the development of dominance relations among *Z. gurneyi* males, using artificial colonies in which individuals of varying sizes and ages are simultaneously or sequentially introduced to one another.

Methods

A general description of the subjects, collecting and rearing, identification of individuals, and observation methods is given in Choe (1994). Stock colonies for this study were collected from Parque

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Nacional Soberania, Panama, between November 1986 and May 1987. The colonies were examined periodically for newly emerged adults, which were immediately transferred to separate rearing chambers. The time and date of emergence, and sex were recorded. Each male was kept in isolation until it was introduced to other males in an experimental colony.

Experiment I: simultaneous introduction. Eight experimental colonies were formed by simultaneously introducing six males of different sizes and ages in each colony. No mating was observed until a dominance hierarchy was established among males in any of the field-collected colonies (Choe 1994) and thus females were not included in the experimental colonies. Each colony was reared in a separate 14-cm-diameter petri dish with a layer of plaster of paris in the bottom. Appleby (1983) demonstrated that a highly linear hierarchy among five or fewer individuals can be obtained by chance alone when the actual dominance relationships are random. The number six was chosen, because in larger colonies it would be logistically difficult to monitor all behavioral interactions.

In order to determine the dominance hierarchy among six males in each colony, five types of intermale interaction [contact avoidance, chasing, head-butting, hindleg-kicking, and grappling (see Choe 1994 for description)] were recorded in terms of frequency, duration, win/loss, and injury. Each colony was observed for 60 h during 5–6 consecutive days.

Experiment II: sequential introduction. In order to allow individuals to emerge at different times, six last-instar nymphs were grouped together to form an experimental colony. Since *Z. gurneyi* nymphs do not appear to recognize relative dominance ranks until they emerge as adults (Choe 1994), males in this experiment were in effect sequentially introduced to each other. A total of eight colonies were formed and observed for intermale interactions in the same way as in experiment I.

Analysis. A separate dominance matrix among males was constructed for each of the 16 study colonies. Spearman's correlation coefficients (r_s) were estimated to determine the relationships between dominance rank and body size (hindfemoral length) or age (male's tenure within the colony). The *G*-test was used for assessing independence in a 2×2 contingency table. 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

Size distribution

The hindfemora of males are longer ($\bar{x} \pm \text{SD} = 0.78 \pm 0.02$ mm, $n = 40$) than females (0.74 ± 0.02 mm, $n = 40$; Mann-Whitney *U*-test, $Z = 6.217$, $P < 0.001$). There were no significant differences in size between these laboratory-reared zorapterans and those collected from the field (Mann-Whitney *U*-test, $P > 0.05$; see Choe 1994 for the data on field-collected zorapterans).

Size versus age

Dominance hierarchies became more or less stable within 2 or 3 days after colonies were formed in both experiments. In experiment I, in which naive males were introduced to one another simultaneously, body size, measured as the hindfemoral length, was highly correlated with dominance rank in all eight colonies (Table 1). Age or tenure, however, was poorly correlated with domi-

Table 1. Spearman's correlations (r_s) of dominance rank with size (hindfemur length) and age (tenure) for eight study colonies of *Zorotypus gurneyi* in experiment I

Colony	Size		Age	
	r_s	Significance	r_s	Significance
I	0.829	$P < 0.05$	0.429	ns
II	0.943	$P < 0.005$	0.829	$P < 0.05$
III	0.886	$P < 0.01$	0.771	ns
IV	0.829	$P < 0.05$	0.657	ns
V	0.943	$P < 0.005$	0.486	ns
VI	1.000	$P < 0.005$	0.829	$P < 0.05$
VII	1.000	$P < 0.005$	0.429	ns
VIII	0.943	$P < 0.005$	0.486	ns

Table 2. Spearman's correlations (r_s) of dominance rank with size (hindfemur length) and age (tenure) for eight study colonies of *Zorotypus gurneyi* in experiment II

Colony	Size		Age	
	r_s	Significance	r_s	Significance
I	0.657	ns	0.943	$P < 0.005$
II	0.429	ns	0.886	$P < 0.01$
III	0.771	ns	1.000	$P < 0.005$
IV	0.829	$P < 0.05$	0.829	$P < 0.05$
V	0.771	ns	0.943	$P < 0.005$
VI	0.886	$P < 0.01$	0.657	ns
VII	0.771	ns	1.000	$P < 0.005$
VIII	0.886	$P < 0.01$	0.943	$P < 0.005$

nance rank (Table 1). Age difference between the oldest and youngest males was 12.4 ± 3.6 days ($n = 8$ colonies). When adult males were allowed to emerge at different times in experiment II, correlations between hindfemoral length and dominance rank were significant in only three out of eight colonies (Table 2). Instead, dominance rank was significantly correlated with male's tenure within the colony, i.e., males that emerged earlier were higher in the hierarchy, in all but one colony (Table 2). In this experiment, the oldest males emerged 16.2 ± 5.1 days ($n = 8$) earlier than the youngest ones.

Dynamics of dominance

In general, males in experiment I showed significantly more frequent interactions (total = 24493, $\bar{x} \pm \text{SD} = 3062.1 \pm 312.9$, $n = 8$) than males in experiment II (19758 , 2467.8 ± 264.3 , $n = 8$; Mann-Whitney *U*-test, $U = 61$, $0.001 < P < 0.002$). Percentage distributions of behavioral interactions among males recorded in both experiment I and II are given in Fig. 1. In both experiments, contact avoidance was the most frequently observed interaction. Head-butting (31.7%) was the second most common behavioral interaction in experiment I, followed by chasing (27.0%). In experiment II, however, chasing (34.4%) was more common than head-butting (22.6%). Although hindleg-kicking and grappling were relatively infrequent, most of them were recorded among

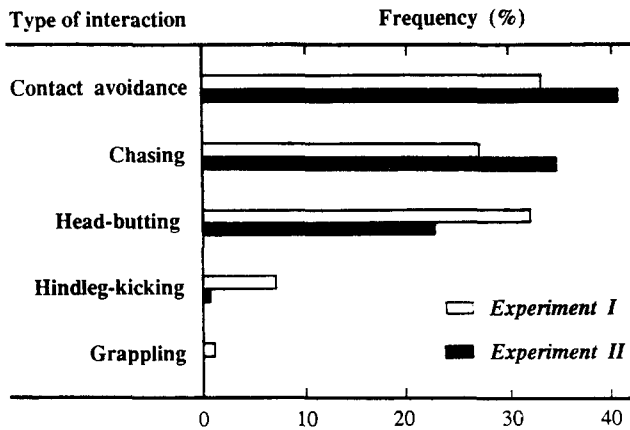


Fig. 1. Frequency distributions of agonistic interactions among *Zorotypus gurneyi* males in experiment I (simultaneous introduction of males; open bars) and experiment II (sequential introduction of males; solid bars)

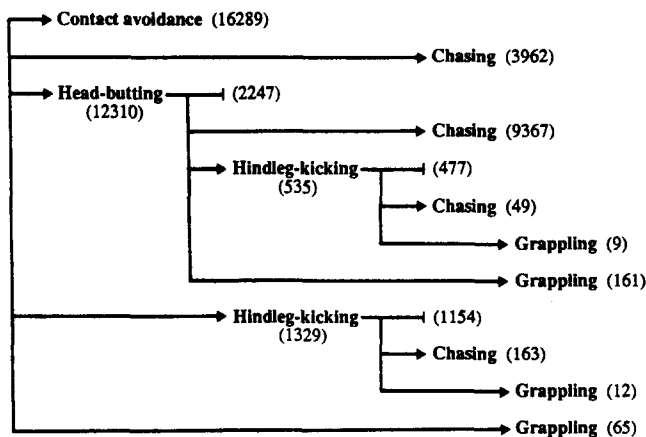


Fig. 2. Behavioral sequences of all agonistic interactions among *Z. gurneyi* males. Figures in parentheses are the numbers of behavioral interactions recorded

males in experiment I. Distribution patterns recorded from the two experiments were significantly different ($\chi^2 = 9.627$, 4 *df*, $P < 0.05$). The majority of head-butting (63.2%), hindleg-kicking (79.9%), and grappling (90.3%) were observed before dominance hierarchies became stable, whereas most contact avoidance (71.2%) and chasing (65.4%) were observed after dominance hierarchies became stable.

Figure 2 shows the sequences of intermale interactions in terms of the numbers of interactions. Data from both experiments were combined for this analysis. Although 26.3% of all grapplings occurred without any preceding behavioral interactions, for the most part (65.2%) males grappled immediately after they butted each other with their heads. Males rarely grappled after they kicked at each other with their hindlegs. Grappling was the most escalated level of agonistic interaction and was not followed by other interactions. Chasing often followed other interactions, mostly head-butting (69.2%), but was never followed by others. Head-butting frequently (81.7%) led to other behavioral interactions.

Injury and the stability of dominance hierarchy

Males in experiment I were injured at much higher rates than those in experiment II. In experiment I, 17 males (35.4%) lost antennal segments, while only 5 (10.4%) did in experiment II ($\chi^2 = 17.08$, $P < 0.005$). Seven males (14.6%) lost one or both hindlegs in experiment I, but no male lost a hindleg in experiment II ($\chi^2 = 36.04$, $P < 0.005$). Among the injured males in experiment I, 2 (4.2%) lost both antennal segments and a hindleg. Nearly half of these injuries (44.8%) were observed to be possible consequences of grapple fights. In colonies I and V of experiment I, the males who established themselves as the dominant males in the early phase of dominance development later descended to the fourth and fifth rank, respectively, probably due to the loss of a hindleg.

Discussion

Determinants of dominance

Size is often considered to be an important variable influencing the outcome of animal contests by game theorists (Parker 1974; Hammerstein 1981) and in general it is positively correlated with observed dominance ranks in a variety of animals (Schein 1975; Wilson 1975). Size is a particularly good predictor of outcome when an experimenter sets up a contest between two animals of different sizes. Chase (1974) argues that a static analysis of dominance hierarchies, i.e., comparing the realized dominance ranks with the predicted ranks based on individual attributes such as size, cannot always explain observed degrees of linearity, although as Jackson and Winnegrad (1988) point out, the individual attributes model by Landau (1951) has not been adequately tested.

Size was no doubt the most important determinant of dominance in *Z. gurneyi*, when males emerged elsewhere were brought together in experiment I. Age did not greatly affect dominance ranks in this experiment, probably because information on each other's age may not have been available to the contestants. Age may be an important factor, but *Z. gurneyi* males may not be able to assess the age of a foreign male. In experiment II, which resembles more closely the natural process of colony development in *Z. gurneyi*, however, age, more accurately tenure, i.e., how long a male has lived in a colony, turned out to be a more important variable than size. Males that emerged earlier could have more fighting experience than the ones that emerged later. As Jackson (1988, 1991) proposed, earlier males' experience of winning might beget more attack initiation and thus more winning. This hypothesis provides a plausible explanation for the results of experiment II except for the two earliest males, because a male that emerged first in a colony could not have opportunities to practise fighting until another male emerged. In all eight colonies in experiment II, the male that emerged first asserted its dominance over the male that emerged second through a series of repeated attacks. This sudden aggression of the first male toward subsequently emerging males was drastically different from the

way it treated the same males when they were all still nymphs. As I reported earlier (Choe 1994), nymphs did not elicit any appreciable level of aggression in adults. The male that emerged first established and maintained its dominance by seeking out and attacking all subsequently emerged males in all eight colonies in experiment II.

As simulated in experiment II, adults emerge throughout the year in *Z. gurneyi* colonies in the field, and newly emerged males, regardless of their relative size, start at the bottom of the hierarchy. Reversals of dominance rank do occur in natural colonies, especially among lower-ranking males, and when they happen it is almost always the bigger males that ascend the hierarchy (Choe 1990). Such experience of winning can certainly override the influence of other factors in determining dominance ranks. A single factor may appear to determine the outcome of agonistic interactions especially in staged combat situations, but it is more likely that multiple factors contribute to hierarchy formation in the course of colony development.

Dominance and life history evolution

In central Panama, *Z. gurneyi* often coexisted with another smaller but more abundant species, *Z. barberi*. A considerable difference in developmental time was noted between these two sympatric species (Choe, unpublished data). Eggs of *Z. gurneyi* eclose approximately 2 weeks faster than *Z. barberi* eggs which take on average 8–9 weeks to develop.

Interestingly, the two species also differ in their mating behavior and system (Choe 1990, 1992). Unlike *Z. gurneyi*, *Z. barberi* males do not form dominance hierarchies. Instead, they exhibit an elaborate sequence of courtship involving nuptial feeding. The mating system in *Z. barberi* appears to be promiscuity by both sexes, and courtship skills and nuptial feeding rather than fighting ability are important determinants of male mating success. Thus early maturity may not give the same advantage to *Z. barberi* males as to *Z. gurneyi* males.

In *Z. gurneyi*, however, selection should favor a shorter development time rather than a greater body size at the time of emergence, because individuals that emerge sooner are more likely to dominate others even in the same cohort. Stearns and Koella (1986) argue that trade-offs between size and age at maturity generally depend upon the rate of development. In *Z. gurneyi*, there is a highly significant correlation between dominance rank and male mating success (Choe 1994) and early maturity has evolved probably due to strong pressure of sexual selection.

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