

Chorus size influences on the anti-predator response of a Neotropical frog

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Leks are perhaps the least well-understood mating system from a functional point of view because males defend neither females nor resources. Instead, males aggregate in a limited area and defend small areas (Davies 1991). Recent reviews of male behaviour on leks have focused primarily on the role of female choice in determining mating success (Balmford 1991). Males that display communally on leks, however, may also benefit in terms of reduced susceptibility to predators. When males group together there is a so-called 'dilution effect', whereby the individual risk of predation is inversely proportional to group size (Hamilton 1971). Individuals grouped for social or foraging reasons can respond adaptively to changes in predation risk that are associated with varying group size. In elk, *Cervus elaphus*, for example, individuals in larger groups are able to devote less time to vigilance behaviour and more time to other activities (Dehn 1990). To our knowledge, the effect of the number of males on a lek on anti-predator behaviour has not been directly investigated.

Male Tungara frogs, *Physalaemus pustulosus*, group together to form choruses and call from stationary positions to attract females. There is no resource-defence and, as with many other frogs, the mating system can be considered a lek (Davies 1991). The main predator of *P. pustulosus* is the fringed-lipped bat, *Trachops cirrhosus*. These bats use the acoustic cues provided by the frog's advertisement calls to locate their prey. Male frogs take evasive action in response to the presence of *T. cirrhosus*, or model replicas, by shutting down calling (Tuttle et al. 1982). This behaviour, however, carries a potential cost because females choose males on the basis of their calls. Males will thus be selected to resume calling as soon as possible. A male's anti-predator response should

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take into account the lower predation risk involved with calling in larger choruses (Ryan et al. 1981). Therefore, we tested whether the duration of non-calling evasive behaviour varies among differently sized choruses because of the change in predation risk.

We conducted experiments in Gamboa, Panama from June to August 1991. Male *P. pustulosus* were introduced into a plastic pool (2.2 m in diameter) containing patches of water (maximum depth of 3 cm) and dry areas, and natural choruses were established. Males were able to leave the pool and numbers were maintained by periodic addition of new individuals. A model of *T. cirrhosus* was made by tracing the wing outline of an individual onto plywood. The model was attached to a roller and run across the pool on a sloped, nylon, monofilament line attached to two wooden stakes (1.7 m and 0.4 m high) spaced 7.2 m apart. Ambient light levels were maintained above those of full-moon conditions by a nearby streetlight, which controlled for variation in responsiveness associated with light levels (Tuttle et al. 1982).

Trials were conducted between 2030 and 2200 hours and 76 trials were performed on 20 nights. There was an interval of at least 10 min between trials. Before each trial, we noted the number of males calling by listening to the chorus. This method limited us to choruses of five or fewer males, but had the advantage that calling was not disrupted. In the field, chorus sizes range from solitary males to several hundred males; solitary males and small choruses are regularly observed. On several nights, more than one trial was conducted, and a few males may have been involved in more than one chorus. However, repeated trials were not made on choruses of the same size and the composition of choruses was unique for all 74 trials. Data on solitary males were completely independent, as these males were removed from the pool after a single trial. Shutdown duration was

Table I. The effect of chorus size on the shutdown duration of choruses

Number of males in chorus	Shutdown duration (s; $\bar{X} \pm \text{SE}$)	Number of choruses
One	11.1 \pm 2.8	16
Two	83.3 \pm 23.8	18
Three	38.5 \pm 8.6	15
Four	16.6 \pm 4.4	15
Five	17.5 \pm 6.2	12

ANOVA, $F_{4,71} = 5.42$, $P < 0.001$.**Table II.** The effect of four experimental treatments on the shutdown duration of solitary males

Loudspeaker treatment	Shutdown duration (s; $\bar{X} \pm \text{SE}$)	Number of males
Bat	5.0 \pm 2.2	10
Bat plus caller	10.9 \pm 6.2	10
No-bat plus Non-caller	15.4 \pm 3.9	10
Bat plus Non-caller	39.2 \pm 12.6	10

ANOVA, $F_{3,36} = 4.17$, $P = 0.012$.

defined as the time that elapsed between the termination of calling after the release of the model and its resumption with the first advertisement call.

Initial results revealed a significant difference in the shutdown durations of solitary males versus two-male choruses. We further investigated this phenomenon by measuring the shutdown duration of solitary males to the model when: (1) the male was alone (Bat); (2) a loudspeaker, placed in the pool, broadcast a conspecific advertisement call every 2 s, mimicking the presence of a conspecific (Bat plus Caller); (3) the loudspeaker broadcast stopped as the model passed overhead, mimicking a conspecific that had responded to a bat (Bat plus Non-caller); and (4) the broadcast stopped without the model being released (No-bat plus Non-caller). Males were tested only once.

Chorus size had a significant effect on calling behaviour (Table I). The shutdown duration of two-male choruses was significantly longer than that of solitary males, four-male or five-male

choruses (Scheffe's test, two-tailed, $P < 0.05$). The shutdown duration of three-male choruses was not significantly different from that of two-male choruses, nor from that of the other chorus combinations. In general, there was a decrease in shutdown duration as chorus size increased from two to five males. The shutdown duration of a solitary male, however, did not differ significantly from that of a five-male chorus.

In *P. pustulosus* the individual risk of predation decreases as chorus size increases (Ryan et al. 1981). Our study shows that the anti-predator response of males is influenced by chorus size over the size range examined. As chorus size increased the anti-predator behaviour of terminating calling weakened, and calling resumed sooner. Male frogs interact vocally and adjust calling behaviour in relation to the presence of conspecifics (Wells 1988). This may provide the proximate mechanism for males to assess chorus size, at least in small choruses.

The loudspeaker experiments investigated potential factors causing solitary males to have a significantly shorter period of shutdown than two-male choruses. Our results showed that the treatments had a significant effect on shutdown duration (Table II). Furthermore, the shutdown duration for the treatment Bat plus Non-caller was significantly greater than that for the other three treatments (ANOVA, $F_{1,38} = 11.79$, $P < 0.001$). Shutdown duration for Bat plus Non-caller was significantly longer than that for No-bat plus Non-caller (Student's *t*-test, one-tailed, $P = 0.04$).

The shutdown duration of solitary males was surprisingly short, given that their risk of predation is greatest. The loudspeaker experiment suggests that the vocalizations of conspecific males provide additional information as to the likelihood that a predator is present. Shutdown duration was longest in the treatment that mimicked a second male alerted to a predator's presence (Bat plus Non-caller). When calls were continuously broadcast, or when the male was alone and the model was passed overhead, he ceased calling for a significantly shorter period. There appears to be a synergistic interaction between cues from a potential predator (in this case, ones from the model passing overhead), and those provided by a conspecific (in this case, switching the loudspeaker off).

Green (1990) noted that male *P. pustulosus* are attracted to conspecific calls. This behaviour

leads to grouping of males and may be related both to benefits derived from the dilution effect and from the increased information provided by a conspecific's response to a potential predator. We suggest that future studies of species that lek, or display communally so that males are in vocal or visual contact, should investigate interactions between males not only in relation to mate attraction, but also in terms of vigilance and other anti-predator behaviour. In many lekking species males possess elaborate ornaments and engage in energetic displays. Interactions between males that reduce predation risks have the potential partially to offset these display costs.

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