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Male whiptail lizards adjust energetically costly mate guarding to male–male competition and female reproductive value

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Simultaneous effects of mate guarding on a male's energy intake and expenditure have not been measured. We tested whether guarding males of the western Mexican whiptail lizard, *Aspidoscelis costata*, reduce energy intake and increase expenditure of energy on male–male aggression. Also, we tested whether guarding males calibrate their aggressive behaviour and feeding to aggression from male rivals (a proxy of their female's probability of extrapair copulation) and body size of the guarded female (positively correlated with fecundity in this species). Observation during and after guarding showed that guarding males (1) ate 77% fewer prey/h and 54% smaller prey, (2) initiated 87% more agonistic interactions/h and (3) participated in 120% more escalated agonistic interactions/h than when alone. Also, guarding males initiated more aggressions when aggression from other males and female size were greater. These results indicate that mate guarding is costly for males because of simultaneous reduction in energy intake and increased expenditure on aggression, and that males incur higher guarding costs when competition with other males and female reproductive value are greater. These costs of mate guarding probably result in negative energy balances that could reduce male fitness through diminished survival. The evolutionary persistence of mate guarding by males can be explained if the net gain in fitness derived from guarding more than offsets its survival costs.

In many species, males accompany females in their fertile or receptive period, usually after copulation. The most commonly proposed benefit for males is supposed reduction in extrapair copulations by females, resulting in an increase in the guarders' probability of fertilizing all or most of their ova (mate guarding hypothesis; Beecher & Beecher 1979; Birkhead 1979). Among several alternative functions (reviewed in Zaldívar-Rae & Drummond 2007), males may accompany females to maintain high rates of copulation and insemination, thus swamping rival sperm or keeping an adequate supply of their own viable sperm at the fertilization site (sperm-loading hypothesis; Alcock 1994), or to court and stimulate females so as to 'convince' them to sustain additional copulations or fertilize their eggs with the companion's sperm (postcopulatory courtship hypothesis; Alcock 1994; Eberhard 1996).

Whatever the benefits, accompaniment probably incurs costs to males in terms of maintenance and survival (Alberts et al. 1996). For example, there is evidence that accompanying males permit closer approach by predators (Cooper 1999) and show reduced predator detection and avoidance (Cooper 1999; Martín & López 1999; Cooper & Vitt 2002; Cothran 2004; Huck et al. 2004), thermoregulation (Saeki et al. 2005) and avoidance of injuries due to aggression from other males (Le Boeuf 1974; Matsubara 2003). Accompaniment may also reduce investment in courtship feeding and copulation (Mougeot et al. 2002), seeking extrapair copulations (Chuang-Dobbs et al. 2001) and attraction of secondary females (Pinxten & Eens 1997). Accompaniment is also associated with reduced body weight or condition (Komdeur 2001; Prenter et al. 2003; Low 2006), slow growth (Robinson & Doyle 1985), reduced stored energy reserves (Sparkes et al. 1996; Plaistow et al. 2003) and short foraging times (Alberts et al. 1996; Matsubara 2003). Energetic costs of current reproductive events may reduce growth rate, survival and ultimately fecundity (Schwarzkopf 1994).

Energetic costs of accompaniment have seldom been evaluated and studies have used only indirect measures of energy intake such as duration of foraging or feeding bouts (Ridley & Hill 1987; Lambrecht 1989; Censky 1995; Alberts et al. 1996; Komdeur 2001; Matsubara 2003), or indirect measures of energy expenditure such as distance travelled or time spent fighting other males (Alberts et al. 1996; Matsubara 2003; Low 2006). In the single study involving a reptile, Censky (1995) found that male companions of the teiid lizard *Ameiva plei* spent less time foraging than solitary males. Furthermore, it has yet to be shown in any species that

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accompaniment both reduces food intake and increases the frequency or intensity of male–male agonistic behaviour.

If accompaniment is costly, individual males should adjust the duration or intensity of accompaniment to maximize net reproductive benefit (Komdeur 2001; Low 2006). This may explain why males stay closer to females and follow them more constantly (probably spending more energy) when females are receptive or ovulating, when density of male rivals is high or when intrusions by rival males are frequent (assuming that accompaniment is mate guarding; Censky 1995; Cooper & Vitt 1997; Cuadrado 2000; How & Bull 2002; Komdeur et al. 1999; reviewed in: Birkhead & Møller 1992, 1998), and why male lizards prolong accompaniment of larger, more fecund females (Cuadrado 1998). Moreover, if accompaniment signals quality to females, male companions may have to invest much time and energy in accompaniment either to persuade females to use their sperm to fertilize their eggs (Alcock 1994; Eberhard 1996), or to obtain other reproductive benefit by keeping close proximity to receptive females.

Male western Mexican whiptail lizards accompany receptive periovulatory females over the substrate at a distance of less than 0.5 m, up to 9 h per day for 1–5 days. During this period, companions follow, court and copulate repeatedly with the accompanied female, and aggressively repel approaching males (Zaldívar-Rae & Drummond 2007). Accompaniment in these whiptails reduces the occurrence of extrapair copulations, so it may function as mate guarding (Zaldívar-Rae 2008). Males court and copulate repeatedly with the females that they accompany, consistent with the sperm-loading and postcopulatory courtship hypotheses (Alcock 1994). However, the copulatory success of companions relative to rival males is not correlated with their share of paternity. Hence, rather than monopolizing paternity, mate guarding may be a male tactic to convince females to grant fertilizations to the companion, which may then further increase his share in paternity by impeding extrapair copulations (Zaldívar-Rae 2008).

By observing field-active individuals, we tested the hypothesis that accompaniment is costly to males in terms of reduced food intake and increased expenditure on male–male aggression. We predicted that males would (1) eat fewer and smaller prey and (2) perform higher rates of agonistic interactions (including both initiated and received aggression) as well as higher rates of escalated aggressions when accompanying females than when they were not accompanying females. In addition, we tested the hypothesis that male companions adjust their feeding and aggressive behaviour in response to the frequency of aggression from male rivals (a proxy of local adult male density and, hence, of the accompanied female's probability of extrapair copulation; see Methods) and the reproductive value of females. Here, we also predicted that male companions would reduce prey ingestion and initiate more aggression (4) as the frequency of aggression from other males increased and (5) as female size increased.

METHODS

Study Area and Species

Isla Isabel is an 82 ha volcanic island 28 km off the Pacific coast of Mexico (21°51′N, 105°53′W). The island's steep rocky slopes and valleys are mainly covered by deciduous dry forest of *Crataeva tapia* trees, *Euphorbia schlechtendalli* bushes, and an understory where cyperaceans predominate. The climate is tropical, with rains in the hurricane season (June–November).

The western Mexican whiptail lizard is medium sized (snout–vent length up to 110 mm), diurnal, terrestrial, wide foraging, insectivorous and nonterritorial. After being courted by a male, a female with ovulatory size follicles becomes receptive and eventually allows copulation (consensual copulations; Zaldívar-Rae & Drummond 2007). From this moment and for the next 1–5 days, the male closely follows the female, repeatedly copulates with her and is aggressive to other males (Zaldívar-Rae & Drummond 2007; this study). There are no obvious visual or behavioural signals in females that indicate the occurrence of fertilization; but males could use chemical cues to ascertain fertilization and suspend accompaniment (Zaldívar-Rae 2008), then seek another periovulatory female (successive female defence polygyny; Zaldívar-Rae & Drummond 2007; Zaldívar-Rae et al. 2008). Eight to 12 days after the end of accompaniment, females deposit and abandon one to five eggs in underground burrow-nests (Zaldívar-Rae et al. 2008). Female snout–vent length and clutch size are positively correlated; hence, larger females may be more reproductively valuable to males (Zaldívar-Rae et al. 2008).

Subjects and General Procedures

In May–July 2003, we haphazardly located 20 male–female pairs and 20 solitary males (definitions below) by slowly walking through forested areas with sparse understory. Paired males measured 86.1–112.4 mm (snout–vent length) and paired females measured 80.0–95.0 mm. Each paired male was observed during one of the 1–4 days that he accompanied a paired female (i.e. remained within 0.5 m of the female, frequently touching and copulating with her), and also during one of the first 4 days after the natural end of accompaniment (mean ± SE = 1.8 ± 0.2 days into the postaccompaniment period). We selected a nearby (within 20 m) solitary male to match each paired male in size; the 20 paired males and 20 solitary males did not differ in length (mean ± SE = 98.47 ± 1.2 mm versus 98.09 ± 1.04 mm, respectively; *t* test for independent samples: $t_{38} = 0.236$, $P = 0.81$) or body mass (25.06 ± 0.99 g versus 25.60 ± 0.86 g; $t_{38} = -0.407$, $P = 0.69$). Note that although solitary males did not accompany a female while we observed them, they may have accompanied females before or after our observations. Habitats of matched males were similar in vegetation type, estimated height of vegetation, vegetation coverage, terrain slope and compass orientation, and type of substrate.

We observed solitary males for a mean ± SE of 2.25 ± 0.28 days after observation of their matched paired males in accompaniment (range 1–5 days; $N = 20$) and 1.1 ± 0.07 days before or after observation of their matched paired males in postaccompaniment (range 1–2 days; $N = 20$). Six of the 20 solitary males were observed while their matched paired male was still in accompaniment. Given the similarities in habitat and proximity between observation dates, we can assume that solitary males and their matched paired males (both during accompaniment and postaccompaniment) faced similar food availability conditions.

We painted all subjects (including paired females) on first sighting and at the start of postaccompaniment observation by squirting yellow 'puff-up' T-shirt latex paint (Glugy™, E. Pérez, Mexico City, Mexico) onto the dorsum from a narrow PVC hose, noting each individual paint pattern. Paint marks lasted 1–2 weeks. Informal comparison with unpainted individuals and pairs in seminatural enclosures revealed no obvious effects of painting on behaviour. Upon completion of observations on each lizard, we measured (snout–vent length) and weighed it, affixed semipermanent glass beads to its tail for individual identification (Fisher & Muth 1989) to prevent us from using the same individual more than once, then released it at its original capture site. We cold-anaesthetized lizards before attaching beads to the tail. Upon completion of the study, we recaptured 53 of our 60 study subjects and removed the bead marks; we could not find the remaining