

# Ownership influences the outcome of male-male contests in the scincid lizard, *Niveoscincus microlepidotus*

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Male snow skinks (*Niveoscincus microlepidotus*) in the Tasmanian highlands have broadly overlapping home ranges, and fight vigorously (often with substantial damage to one or both participants) upon encountering another adult male. We observed 32 male-male contests, involving at least 49 different males, during a five-year field study near the summit of Mount Wellington. Bouts involving similar-sized lizards typically continued for longer than bouts involving a greater size disparity between the combatants. Resident males won 72% of all bouts, despite a lack of any significant difference between residents and intruders in body sizes, relative head sizes or body condition. Thus, prior residency of a site appears to be the major determinant of success in male-male rivalry. *Key words*: male-male contest, ownership, lizard, *Niveoscincus microlepidotus*. [*Behav Ecol* 11:587–590 (2000)]

Comparative evidence suggests that agonistic interactions among males favor the evolution of traits such as large body size, weaponry and the ability to make tactical fighting decisions (Andersson, 1994; Bradbury and Vehrencamp, 1998; Darwin, 1871; Dugatkin and Reeve, 1998). This result receives strong support from studies of behavioral ecology, which show that asymmetries in such traits often determine the outcome of animal conflicts (Andersson, 1994). Even secondary traits that covary with the primary determinant of fighting ability may be used by a potential combatant to estimate his rival's fighting ability, and on this basis decide whether to pursue the contest (Bradbury and Vehrencamp, 1998; Enquist and Leimar, 1983, 1987).

Agonistic interactions are, however, not always resolved by straightforward asymmetries in traits important for physical fighting. Instead, differences in the value of the contested resource to the participating combatants may form the basis for tactical contest decisions. For example, starved trout (*Salmo trutta*) are more competitive in contests over food than are fish fed to satiation (Johnsson and Björnsson, 1994). Thus, motivation to engage in risky fighting behavior may increase as an individual's resource levels decline. Furthermore, previous investments into a resource, such as time for courtship, mate guarding and investment into spermatozoa and seminal fluids, may also motivate an animal to engage in contests to a higher level of escalation, such as in sand lizards (*Lacerta agilis*; Olsson, 1994). The value of the resource is also set by the frequency with which it is encountered. When resources are commonplace, selection for simple rules of thumbs for how to resolve conflicts may be the result. A classical example of this is the "owner wins" tactics in interactions between thermoregulating speckle-wood butterflies for a "place in the sun" (Davies, 1978, but see also Wickman and Wiklund, 1983).

Prior to statistical analysis becoming commonplace in biol-

ogy, Rand (1967) performed a detailed, graphically based exploratory data analysis of fighting behavior in male *Anolis lineatopus*. He came to the conclusion that males incorporate information about both residency and size of opponents when deciding whether to escalate or withdraw in contests (Rand, 1967). Other studies suggest that lizard contests may be settled by residency (Leuck, 1995; McMann, 1993, in captive populations), asymmetries in body size (Olsson and Madsen, 1998), more rarely in age (Olsson and Shine, 1996), and in several taxa by differences in nuptial coloration between the contestants (Olsson, 1994; Olsson and Madsen, 1998; Thompson and Moore, 1991; review in Bradbury and Vehrencamp, 1998). However, to the best of our knowledge there are no published analyses where data are detailed enough to admit robust tests of effects of ownership in escalated contests in a natural population of a reptile species (Olsson and Madsen, 1998). Indeed, there have been relatively few analyses of effects of ownership where confounding variables (e.g., body size) are controlled for in any animal species in the wild (Bradbury and Vehrencamp, 1998; Riechert 1998, Table 1, p. 68).

In the present study of the Tasmanian snow skink (*Niveoscincus microlepidotus*), we analyze data on agonistic interactions between free-ranging, unmanipulated male lizards. The study system that we have used (snow skinks in the Tasmanian highlands) facilitates the investigation of this topic. Snow skinks are not strictly territorial and frequently cross into other males' home ranges in their searches for prey and partners (Olsson and Shine, unpublished data), which leads to conflicts between males (and sometimes between females). Furthermore, snow skinks tend to be relatively long-lived (up to 12–13 years, Hudson, 1996) and, hence, the acquisition of a resource may incur a long-term benefit in several respects, such as opportunities for thermoregulation, shelter, and the acquisition of partners. Additionally, most of the agonistic interactions between male snow skinks occur immediately after they emerge from hibernation, about 3 months before the mating season (Olsson, Birkhead, and Shine, 1999). Thus, males defend actual sites per se, rather than, for example, guarding receptive females.

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**Table 1**  
**Mean trait values compared by residency status and contest success with relevant test statistics**

Variable	Residency status		Contest success							
	Resident	Intruder	<i>t</i>	<i>N</i>	<i>p</i>	Winner	Loser	<i>t</i>	<i>N</i>	<i>p</i>
Mass (g)	3.87 ± 0.56	3.86 g ± 0.55	0.04	30, 27	.96	3.94 ± 0.51	3.77 ± 0.51	1.25	30, 27	.21
SVL (mm)	62.1 ± 3.49	61.7 ± 2.99	0.45	30, 27	.65	62.4 ± 3.39	61.4 ± 3.04	1.20	30, 27	.24
Head length (mm)	11.83 ± 0.50	11.70 ± 0.60	0.78	30, 27	.56	11.83 ± 0.54	11.70 ± 0.65	0.88	30, 27	.38
Head width (mm)	8.52 ± 0.57	8.60 ± 0.50	0.59	30, 27	.56	8.53 ± 0.56	8.58 ± 0.52	0.32	30, 27	.75
Condition index	-0.02 ± 0.71	0.02 ± 0.35	0.47	30, 27	.64	0.02 ± 0.42	-0.03 ± 0.30	0.52	30, 27	.62

Trait values are given as mean ± SD.

## METHODS

Snow skinks (*Niveoscincus microlepidotus*) are small (to 70 mm snout-vent length, 5 g) viviparous scincid lizards that are restricted to high-elevation rocky habitats on the island of Tasmania, southeast of the Australian mainland. We studied a population of this species at 1270 m elevation on Mt. Wellington, ca. 15 km S Hobart, for five years (1993–1997). The population was monitored from the time the lizards emerged from hibernation (in September/October) until they returned to their winter quarters in April the following year. The study site was characterized by rocky dolerite outcrops interspersed with hardy vegetation and the honey Richea bush, *Richea scoparia*, that produces nectar on which the lizards forage throughout the flowering season (ca. December–February, depending on climatic conditions; Olsson M and Shine R, in preparation).

A more detailed description of the methods we used has been published elsewhere (Olsson and Shine, 1998 and Olsson *et al.*, 1999) and we, therefore, only give a short summary here. Snow skinks have no sexually dimorphic conspicuous coloration (to the human observer) and, hence, the cues to a rival's intentions and fighting ability come solely from his body size and behavioral displays. We only quantified morphological traits relevant for a male's fighting ability, such as body size and head dimensions. Upon emergence from hibernation the lizards were caught by hand or by noosing. We then measured snout-vent length (heretoforth SVL) and total length to the nearest mm, and head length and head width to the nearest 0.01 mm, and weighed each lizard to the nearest 0.01 g before release. Residual scores from the general linear regression of ln mass versus snout-vent length were used as our index of body condition in further analyses. The lizards were marked by placing an oval tape marker (TESA tape, Germany) on their back with an individual number. The temporary tape marker usually remained on a lizard's back until its subsequent skin-shedding.

Lizard contest behavior was monitored by watching males interact naturally in the wild. Our observations of male movements indicate that males of this species are not strictly territorial; instead, they have overlapping home ranges. Nonetheless, each male's home range typically contained one or more sites (used for shelter or basking) in which we regularly observed this animal, and no other male. Thus, we could unambiguously assign each male as either a "resident" or an "intruder" at the time of the contest. We then monitored the duration of the interaction (using a wristwatch) and identified which male won the battle. All battles had clear victors, with the winner chasing the loser out of the disputed area.

## RESULTS

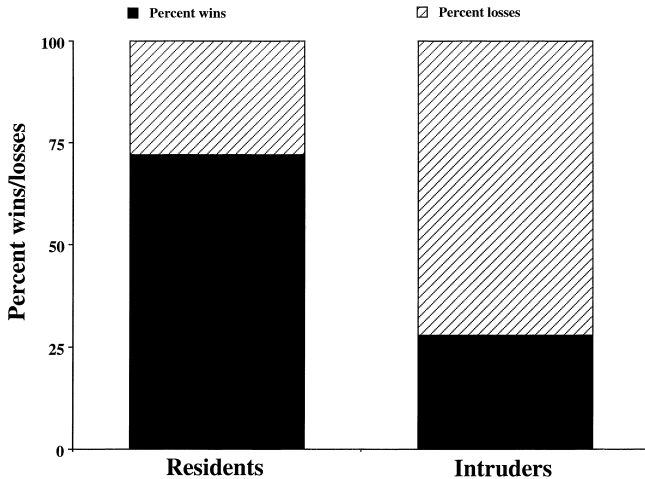
We observed 32 interactions involving 49 males for which we could determine identity during the study period. For some

contests, we failed to capture one of the interacting males. Thus, the sample sizes for morphological traits in Table 1 differ slightly between the categories. When interactions were separated by more than 2 days, we assumed that contest observations were independent of male identity. Therefore, in a few cases we have used more than one data point per individual male (mean = 1.1 observations/individual, SD = 0.46, range 1 to 3). Three males occurred both as intruders and residents in different contests. Excluding these males did not alter the results in any significant way and they have therefore been left in for the analyses reported on in the present article. Furthermore, no males were "floaters" or were transients migrating through the study site.

Male contests varied considerably in the degree of escalation and duration. Most interactions were resolved by displays, wherein each male turned sideways towards the rival with dorso-lateral distension (median display time equaled one s, mean = 63.0 s ± 244.0, *N* = 29). The combat was resolved without physical contact in most of these cases. However, in other contests males fought viciously for up to 20 min, with severe injuries to at least one of the contestants. In several cases, males lost toes and in one instance, an entire foot was torn off. Thus, some fights entail high costs to the interacting males.

Resident males were no larger in bodily dimensions than were intruding males (see Table 1). This result accords well with our preliminary observations that geographic areas were not exclusively monopolized by large dominant males, as is the case in many other lizard species (reviewed by Olsson and Madsen, 1998). Instead, most interactions between males occurred as a consequence of one animal wandering into another male's home range during foraging bouts and/or searches for partners. Thus, effects of ownership were not confounded by a consistently larger body size of the resident male (see Table 1). We also used paired *t* tests to analyze data for encounters where we captured both participants, to provide a more direct comparison between the individuals involved in each combat bout. There was still no significant difference between intruders and resident males in body dimensions (e.g., for SVL, mean difference = 0.4 mm, *t* = .50, *p* = .62; body mass difference averaged 0.02 g, *t* = .13, *p* = .89).

The data in Table 1 were analyzed by *t*-tests, strongly suggesting that there was no consistent difference in body size (SVL, mass), relative head length or body condition (mass relative to length) between "winners" and "losers" of male-male contests. These analyses were supported by paired *t*-tests, yielding similar results: the average differences between residents and intruders were 1.26 mm in SVL (± 0.84, SE), 0.22 g in body mass (± 0.16, SE), 0.12 mm in head length (± 0.18, SE), 0.09 mm in head width (± 0.17, SE) and 0.02 in body condition (± 0.09, SE). None of these differences in body dimensions between residents and intruders deviated significantly from zero (0.15 < *p* < .87; *N* = 23). Instead, residency



**Figure 1**  
Effect of residency on the outcome of contests in male snow skinks.

determined contest outcomes. Out of 32 resident males observed in contests, 23 (71.9%) were scored as winners and nine (28.1%) as losers (Figure. 1; against a null of equal probabilities of success for each type of male, chi square = 6.1,  $p = .02$ , DF = 1).

Game-theory suggests that when the size difference between two rivals increases, less time will be necessary to establish which male has the higher fighting ability and thus, who should withdraw before being injured (e.g., Enquist and Leimar, 1983). Our data support this prediction: The smaller the absolute size difference between rivals, the longer the contest ( $r_s = -.33$ ,  $p = .05$ ,  $N = 24$ ; one-tailed test). Game theory models such as the sequential assessment game (Enquist and Leimar, 1983) also predict that the longest contests will occur when the resident is marginally smaller than the intruding rival. This prediction derives from the idea that the asymmetry in ownership and previous investment motivates the resident to prolong the fight and take greater risks when defending his resource. Anecdotal observations from our study does not support this prediction. The resident lizard was heavier than the intruder (by 3.6% and 9.9% in body mass respectively) in both of the two longest fights that we recorded (lasting 20 min, and 9 min and 45 sec respectively).

## DISCUSSION

Our data provide a reptilian example whereby success in a male-male contest is determined not by an animal's fighting ability (as determined by size, etc.), but by ownership (or some trait relating to it). Nonetheless, although the literature contains several examples of this phenomenon in many taxa from isopods to birds, few of these are from natural populations (Riechert, 1998; Table 1, p. 68).

We doubt that snow skinks are unique among reptiles in showing ownership-effects on the outcome of contests. The difficulty of observing male-male contests of free-ranging reptiles, especially involving unmanipulated animals, means that there are virtually no empirical data with which to investigate the issue in a natural population (but see Olsson 1992; Rand, 1967; review of studies in captivity in Olsson and Madsen, 1998). The lack of comparative evidence makes it difficult to speculate on the conditions that favor the "owner wins" rule in snow skink contests. Furthermore, in some of the best studied taxa there is conflicting evidence as to what degree of ownership determines the outcome of contests. In an English population of the speckled wood butterfly (*Pararge aegeria*),

the convention "owner wins" seemed to be generally adopted (Davies, 1978). In a Swedish study of the same species, however, removed owners were engaged in a prolonged spiral flight on rerelease on their former territory and, although the original territory owner eventually got his territory back, a different convention with respect to escalation appeared to rule (Wickman and Wiklund, 1983). Davies suggested that in the English population, warm sunny spots were more plentiful than in a cold Swedish spring and, hence, resource values differed between the two sites (see discussion of this and related example in Bradbury and Vehrencamp, 1998, pp. 712–720). A similar argument may apply in snow skinks to a greater degree than in many other reptiles. In their severely cold environment, a home range with a protected basking site is likely to be crucially important to organismal fitness. Given the very high population densities of lizards at our study site (several hundred/ha; Olsson and Shine, unpublished data.), very few such sites are unoccupied. Thus, a resident has much to lose from being displaced, where the intruder has the option of simply returning to his usual home-site. Such circumstances may generate a substantial asymmetry in the value of the resource (the basking site) to the two participants, and thus favor considerably enhanced motivation for the resident to escalate contests. The enhanced probability of successful basking-site defense could even result in an on average elevated body temperature of a resident, thereby making him a more successful fighter (Edsman L, unpublished data, cited in Olsson and Madsen, 1998).

An alternative hypothesis to the higher incidence of wins in resident than in intruder males is that resident males are simply better fighters than are intruders and that this quality is independent of male size. In several other species, such as Midas cichlids (*Cichlasoma citrinellum*; Barlow *et al.*, 1986) and tree lizards (*Urosaurus ornatus*; Thompson and Moore, 1991), fighting ability is strongly influenced by some innate level of aggression. This could, for example, be set by plasma levels of testosterone, corticosteroids, or growth hormone that we did not sample in the present study. If lizards differ in this way, better fighters may be more likely to defend sites against intruders. However, this hypothesis seems unlikely to explain the snow skink data because intruders were not "homeless" but males defending adjacent sites (i.e., being residents under such conditions).

In conclusion, male snow skinks engage in contests that may involve a high level of risk in the sense that entire limbs may be torn off during its escalated phase. Our data demonstrate that fights do escalate between residents and intruders and, hence, although resident males win more contests, there is no strict adoption of the rule "owner wins." Although we could not detect a size difference between intruders and resident males, we cannot rule out the possibility that there is a difference in some other aspect of fighting ability between the two categories of males that also contributes to the success of resident males. However, the primary determinant of male-male contests in lizards has been repeatedly demonstrated to be body size (Olsson and Madsen, 1998). Because this factor can be ruled out in the present study, there seems to be little doubt that ownership plays a significant part in determining the outcome of contests in this species.

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