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State-dependent decisions in nest site selection by a web-building spider

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Foraging decisions may reflect a trade-off between food intake and safety and can also be influenced by the animal's internal state. Foraging in the web-building spider *Stegodyphus lineatus* depends on a capture web associated with a retreat (the nest). The relocation of nests, including the take-over of conspecific nests, may be viewed as a foraing decision, which depends on risk of exposure, cost of silk production and hunger state. We investigated a possible state-dependent trade-off in nest site choice of *S. lineatus* spiderlings. The philopatric nature of *S. lineatus* implies a high risk of encounters with potentially cannibalistic conspecifics and a potential loss of inclusive fitness because encountered conspecifics are likely to be kin. To test for state dependence of foraging decisions, we compared preferences of well-fed and hungry spiders for their own nests and those of siblings and nonsiblings. We expected satiated spiders to prefer their own to conspecific nests and hungry spiders to choose the risky option of a conspecific nest. Since *S. lineatus* is less aggressive towards kin, we tested the ability of spiders to discriminate kin by silk-bound cues. Because of this reduced aggression, preference for kin nests should be safer than preference for nonkin nests. A strong preference for self-nests demonstrated self-recognition in well-fed spiders. However, neither well-fed nor hungry spiders discriminated between nests of siblings and nonsiblings. Well-fed spiders preferred self-nests to empty chambers, but showed no discrimination between nonself-nests and empty chambers. Hungry spiders showed a reduced preference for self-nests, suggesting that hunger elicits a more risky foraging strategy. A tendency of hungry spiders to adopt the nests of conspecific spiders may reflect a silk-saving strategy. We conclude that *S. lineatus* spiders show state-dependent decision making in nest site selection.

Analyses of foraging decisions are often based on the question of whether animals attempt to maximize intake rates. Studies of spiders that relocate webs in response to prey capture rate provide support for such maximization models (e.g. Janetos 1982; Olive 1982; Nakata & Ushimaru 1999). Optimal foraging behaviour, however, may encompass other, conflicting, activities such as antipredator behaviour that lead animals to trade food intake rate against other activities (Krebs & Kacelnik 1991). For example, spiders trade food intake against costs of web building, predation and aggressive interactions with conspecifics (Uetz 1992, 1996; Pasquet et al. 1999). Smallwood (1993) showed that aggression among conspecifics in high-density patches was a better predictor of web site tenure in the orb-weaving spider *Tetragnatha elongata* than was risk-sensitive foraging based solely on variance in food availability (Gillespie & Caraco 1987). Since most spiders are territorial and aggressive towards conspecifics, individuals inhabiting high-density patches should adjust their foraging behaviour to decrease the risk of predation (Burgess & Uetz 1982; Rypstra 1983; Smallwood 1993).

Decision making based on trade-offs may be influenced by the internal state of the animal (Krebs & Kacelnik 1991; Uetz 1992). If the animal is near starvation, the motivation for feeding should be higher than when it has large body reserves. Thus, hungry animals may be more willing to risk predation while foraging than satiated animals (Krebs & Kacelnik 1991).

We investigated state-dependent foraging decisions in the web-building spider *Stegodyphus lineatus* Latreille

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(Eresidae). Foraging in *S. lineatus* depends on two- or three-dimensional capture webs constructed with cribellate silk, while the spider occupies solid, conical nests (retreats) that are always associated with the capture web. We use the term ‘nest’ to refer to the retreat and the associated capture web. Decisions to relocate nests may be based on the cost of silk production (Pasquet et al. 1999), risk of mortality associated with exposure and movement (Ward & Lubin 1993) and internal state such as hunger status (Janetos 1982). As an alternative to relocation and construction of new nests, *S. lineatus* may take over nests of conspecific spiders (Ward & Lubin 1993). The benefits of taking over a conspecific nest are the possibility of adopting a successful foraging patch and the reduced expense of nest construction, while take-overs can be risky in the light of a potentially fatal encounter with a resident spider. The young of *S. lineatus* are philopatric and may be found at high densities near the maternal nest (Lubin et al. 1998; Johannesen & Lubin 1999). Such heterogeneous distribution makes frequent encounters with potentially cannibalistic conspecifics likely, which may have implications for foraging strategies. In a series of nest preference experiments where spiderlings were given a choice between their own nest and a conspecific nest, we investigated the hypothesis that a trade-off between safety and foraging would depend on the hunger state of the spider. We expected well-fed spiderlings to select their own nest, while a reduced preference for their own nest by hungry spiders would suggest a trade-off between safety and foraging.

The philopatric nature of *S. lineatus* implies that a neighbour is likely to be close kin, a prediction supported by genetic analyses (Johannesen & Lubin 2001). Cannibalism could therefore impose a loss of inclusive fitness (Pfenning 1997). The presence of kin recognition in this species was suggested by previous results showing nonkin-biased cannibalism (Bilde & Lubin 2001). Kin recognition should help avoid loss of inclusive fitness by reducing aggression towards relatives. We tested the ability of *S. lineatus* to recognize self, kin and nonkin through silk-bound cues by presenting spiderlings with the choice between two nests in trials comparing (1) self versus nonsibling, (2) self versus sibling and (3) sibling versus nonsibling. We further investigated whether spiders were attracted or repelled by silk from self, siblings and nonsiblings in ‘empty-chamber trials’ where the spider was given a choice between either a self or conspecific nest and an empty chamber. Because cannibalism is reduced among kin, nests of siblings should be safer than nests of unrelated spiders (Bilde & Lubin 2001). In spiders, pheromones associated with silk play an important role in communication systems and are likely to provide kin recognition cues (Witt & Rovner 1982; Pollard et al. 1987). Clark & Jackson (1995), for example, found differential preference for draglines produced by familiar spiders of a jumping spider *Portia labiata* suggesting recognition of individual conspecifics based on silk-borne cues. In *S. lineatus*, the ability to assess kinship through silk-bound cues would facilitate decision making before a potentially dangerous encounter with the resident spider.

METHODS

Study Species

The subsocial *S. lineatus* Latreille (Eresidae) has a circum-Mediterranean distribution where it occupies arid and semiarid regions. This species is usually annual and semelparous with extensive maternal care and matriphagy. The female releases the young (40–140 spiderlings) from the egg sac and feeds them actively by regurgitation for ca. 2 weeks. The spiderlings then consume their mother, and stay in the maternal nest for a further 2–4 weeks before the first individuals initiate dispersal (D’Andrea 1987). Philopatry and a low dispersal ability result in a clustered distribution and subdivided population structure (Johannesen & Lubin 1999).

We collected 134 subadult *S. lineatus* from a desert habitat near Jerusalem in March 2000 and brought them to the Sede Boqer Campus, Ben Gurion University, in the Negev Desert. Spiders were kept individually in plastic containers with mesh lids (height 10 cm, diameter 5 cm) and reared to maturity on a diet of desert locusts, *Locusta migratoria*, crickets, *Acheta domestica*, and flour beetles, *Tenebrio molitor*. We kept the spiders outdoors under natural temperature and light conditions, partially protected against direct sun by shade cloth. We obtained 73 males and 61 females. Females were mated, produced egg sacs and were eventually consumed by the spiderlings (matriphagy is typical in this genus), while the males died naturally shortly after mating. Juvenile spiders were assigned to experiments when the majority of spiderlings had left the maternal nest, ca. 2 weeks after the first dispersing individuals. After the experiments in January 2001, we released the spiderlings into their natal habitat.

Experimental Procedure

Spiderlings were placed individually in cylindrical plastic chambers (height 5 cm, diameter 1.5 cm) and allowed to build nests for subsequent use in the preference experiments. Approximately once a week they were fed three or four wild type fruit flies *Drosophila melanogaster* reared in laboratory cultures. We tested spiders under well-fed and hungry treatment conditions; well-fed spiders were given prey 1–2 days before the nest choice experiments while hungry spiders were deprived of food for 12–14 days prior to trials. All experiments were performed in the laboratory under standardized conditions of 26 ± 1°C and a natural light:dark regime. Table 1 summarizes the combinations of trials and number of replicates.

For the nest choice experiments we used T-shaped vials consisting of a central plastic container (height 5 cm, diameter 2.5 cm) with two cylindrical chambers (height 5 cm, diameter 1.5 cm) attached, one or both chambers (randomly chosen) containing a spider’s nest according to the experimental protocol (Table 1). We removed spiders from their nests immediately before each choice experiment and attached the chambers to the central container. The test spider was then placed in the central chamber and left to choose a web site. Since *S. lineatus* are nocturnal we started all trials in the evening and allowed

Table 1. Summary of experiments

State	Chamber 1	Chamber 2	*N*
Well fed	Sib nest	Nonsib nest	33 (38)
Hungry	Sib nest	Nonsib nest	32 (37)
Well fed	Self-nest	Nonsib nest	32 (44)
Hungry	Self-nest	Nonsib nest	28 (35)
Well fed	Self-nest	Sib nest	25 (31)
Well fed	Self-nest	Empty	30 (39)
Hungry	Self-nest	Empty	25 (49)
Well fed	Nonsib nest	Empty	29 (40)
Hungry	Nonsib nest	Empty	35 (44)
Hungry	Sib nest	Empty	23 (30)

Stegodyphus lineatus spiderlings were given a choice between two nests or between a nest and an empty chamber. The nests originated from the spider itself (self-nest), a sibling (sib nest) or an unrelated conspecific (nonsib nest). Experiments were performed in test vials with two chambers and with either well fed or hungry spiderlings (state); *N*=number of replicates in a trial where spiderlings made a choice; numbers in parentheses are the sums of *N* and replicates in which no choice was made, the latter being excluded from the analyses.

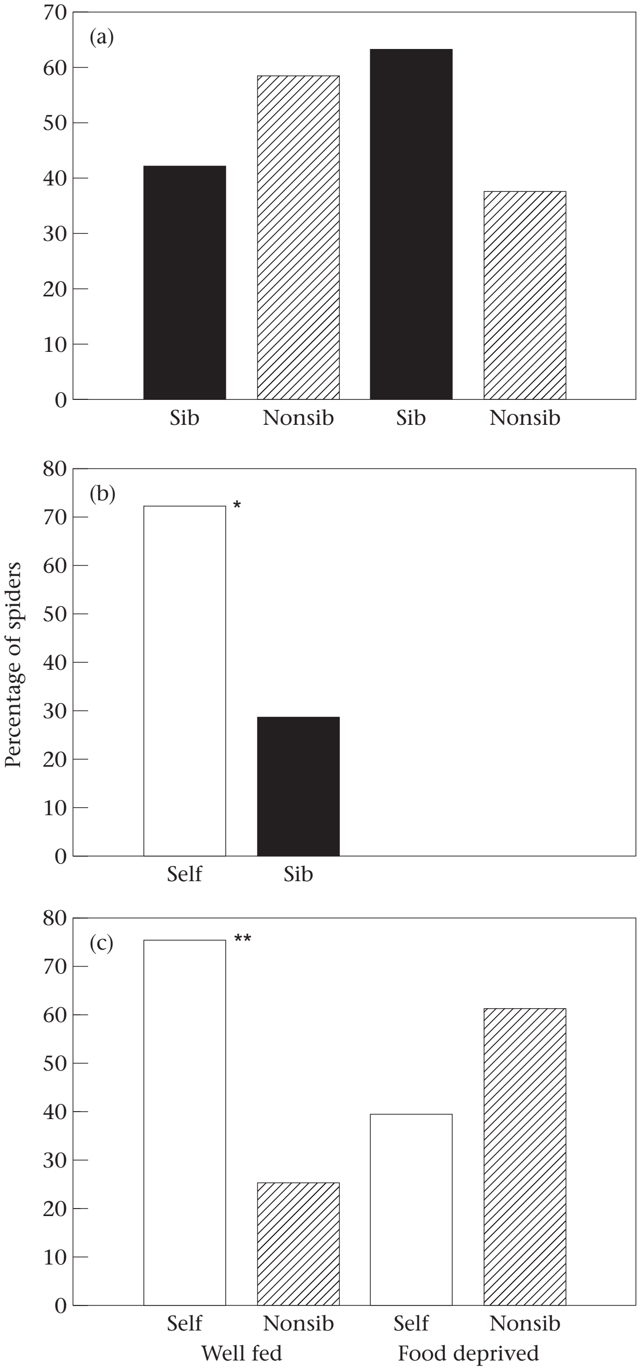

Figure 1. The results of preference experiments where well-fed and food-deprived *Stegodyphus lineatus* spiderlings were given a choice between two nests, which could be their own nest (□), the nest of a sibling (■) or the nest of an unrelated conspecific (▨). (a) Sib nest versus nonsib nest (well fed: $\chi^2_1=0.758$, $P=0.384$; food deprived: $\chi^2_1=2.0$, $P=0.157$). (b) Self-nest versus sib nest ($\chi^2_1=4.84$, $P=0.028$). (c) Self-nest versus nonsib nests (well-fed: $\chi^2_1=8.0$, $P=0.005$; food deprived: $\chi^2_1=1.286$, $P=0.257$).

the spiders to choose a nest site over night. The following morning we recorded the nest choice of the spiders.

Prior to each experiment we weighed the spiders and matched them so the maximal weight difference between the test spider and the spider(s) whose nest was used in the replicate was 0.5 mg (weight range of experimental spiders was 2.5–5 mg). In all replicates, we used test spiders of similar age originating from different families. We controlled for spider size and age to eliminate their possible effect on silk properties that could influence the nest choice of spiders.

We analysed the results with tests of independence, excluding those replicates where spiders made no choice (i.e. remained in the central chamber). We applied logistic regressions to analyse the effect of feeding condition on nest site preferences by comparing trials with fed and hungry spiders.

RESULTS

The spiderlings showed no discrimination between nests of siblings and unrelated conspecifics (Fig. 1a), irrespective of hunger state (comparison of well-fed and hungry spiders in the sib–nonsib trial, logistic regression: $G_1=2.64$, $P=0.104$). In contrast, well-fed spiders showed a strong preference for their own nest over the nests of siblings (Fig.1b) and of unrelated spiders (Fig. 1c). When hungry, however, more spiders preferred the nest of a nonsibling to the self-nest (Fig. 1c). Thus, there was a shift in preference from self-nest in well-fed spiders towards a nonsibling's nest in hungry spiders (comparison of well-fed and hungry spiders in the self–nonsibling trial, logistic regression: $G_1=7.99$, $P=0.005$).

Well-fed spiders also preferred their own nest in empty-chamber trials (Fig. 2a). When hungry, more spiders selected the empty chamber indicating a tendency to select a novel web site (comparison of well-fed and hungry spiders in the self–empty trial, logistic regression: $G_1=3.82$, $P=0.051$; Fig. 2a). In nonsib versus empty-chamber trials we found opposite trends (Fig. 2b). Fed spiders showed no evidence of preference while hungry spiders selected the nest of unrelated conspecifics, again

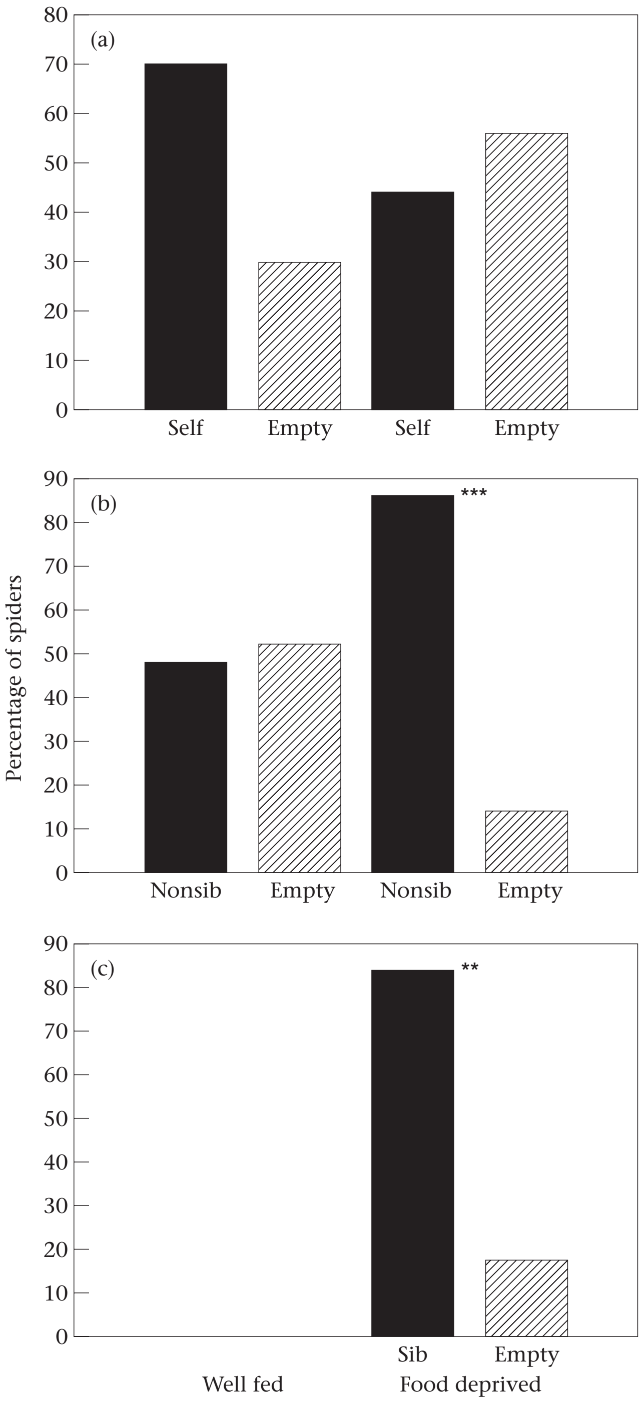

Figure 2. The results of preference experiments where well-fed and food-deprived *Stegodyphus lineatus* spiderlings were given a choice between a spider's nest and an empty chamber. (a) Self-nests (well fed: χ^2_1=4.8, P=0.028; food deprived: χ^2_1=0.36, P=0.549. (b) Nonsib nests (well fed: χ^2_1=0.034, P=0.853; food deprived: χ^2_1=17.857, P<0.001). (c) Sib nests (χ^2_1=9.783, P=0.002).

resulting in a state-dependent shift in preference for nest site (comparison of well-fed and hungry spiders in the nonsib–empty trial, logistic regression: G_1=10.62, P=0.001). The tendency for *S. lineatus* to select the nest of conspecific spiders in poor food conditions was supported in the sib versus empty-chamber trial, where spiders preferred the nest of a sibling (Fig. 2c).

DISCUSSION

Stegodyphus lineatus spiderlings showed a consistent preference for their own nest in good food conditions, revealing the ability to discriminate between self and nonself (whether sibling or nonsibling). Hungry spiders showed reduced preference for their own nest and were equally likely to choose the self-nest as the conspecific nest. The results from empty-chamber trials confirmed that food-deprived spiders were more inclined to select a novel nest site. This is consistent with a number of studies reporting decreased giving-up times leading to frequent relocation of web sites in response to low prey capture rate (e.g. Janetos 1982; Olive 1982; Rypstra 1983; Nakata & Ushimaru 1999). The choice of a novel web site by hungry spiders suggests that a decision is made based on previous experience, namely, the lack of foraging success associated with their former web site. Furthermore, it suggests a state-dependent change of foraging strategy where safety is traded for foraging (Milinski & Heller 1978; Dill & Fraser 1984; Gilliam & Fraser 1987; Wright et al. 2001).

The spiderlings preferred to take over conspecific nests rather than construct new webs in empty chambers. The cost of web construction may be high and thus is likely to play a major role in decisions involving web relocation (Janetos 1986; Tanaka 1989). The nest of *S. lineatus* is likely to be a valuable resource with a permanent retreat that is expanded through the season. All activities, such as feeding, mating and provisioning of young, take place in the nest, which also provides protection against predators (Konigswald et al. 1990; Henschel et al. 1992). The spiders are philopatric and extremely sedentary: Ward & Lubin (1993) found that only 32% of spiders moved between nest sites and the majority of these moved only once. This is a low rate of movement in comparison with many other web-building spiders (Janetos 1982; Gillespie & Caraco 1987; Tanaka 1989; Nakata & Ushimaru 1999). Web relocation may be especially costly in *S. lineatus* because of the considerable risk of mortality when the spiders are exposed during movement (Vollrath 1985; Lubin et al. 1993; Ward & Lubin 1993) and high cost of web renewal (Prestwich 1977; Tanaka 1989). Pasquet et al. (1999) showed that *S. lineatus* spiders lose 3–7% of their body weight during the construction of a capture web of average size, and the old cribellate silk is not recycled. Furthermore, because the spider invests time in web construction it may incur costs of missed foraging opportunities (Stephen & Krebs 1986; Pasquet et al. 1999). These considerable costs may explain the tendency of *S. lineatus* to take over conspecific webs as a silk-saving strategy. Take-over of conspecific or heterospecific nests or webs in the field is a common behaviour in spiders (Janetos 1986; Nentwig & Heimer 1987; Smallwood 1993). *Stegodyphus lineatus* were found in nests of conspecifics in their natural habitat and nest take-overs were not uncommon (Ward & Lubin 1993). A closely related species, *Stegodyphus dufouri*, frequently occupies conspecific nests or even shares nests (personal observations).

There was no evidence that *S. lineatus* spiderlings discriminated between nests of siblings and nonsiblings. In empty-chamber trials, hungry spiders were equally likely to select either. It is possible that *S. lineatus* does not distinguish silk from kin and nonkin or that discrimination is not necessary in a situation where there is no direct interaction with conspecific spiders. Smallwood (1993) found that intruding *T. elongata* spiders could take over conspecific webs by chasing away the resident spider. If the resident spider is likely to be related, the ability of the intruder to discriminate kin should be selected for, unless the direct fitness benefit of cannibalizing kin is larger than the loss of indirect fitness.

In summary, *S. lineatus* show different foraging modes in response to hunger state. Well-fed spiders show greater web site tenacity and self-recognition allows for discrimination between their own and conspecific nests. In response to hunger, spiders apparently adopt a more risky foraging strategy of selecting novel web sites at the expense of safety. We interpret the tendency to take over conspecific nests as a silk-saving strategy, suggesting that the cost of web production plays a role in foraging decisions in addition to a state-dependent trade-off between safety and foraging.

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