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Alternative predatory tactics of an araneophagic assassin bug (*Stenolemus bituberus*)

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Abstract Predators of dangerous prey risk being injured or killed in counter-attacks and hence may use risk-reducing predatory tactics. Spiders are often dangerous predators to insects, but for a few, including *Stenolemus bituberus* assassin bugs, web-building spiders are prey. Despite the dangers of counter-attack when hunting spiders, there has been surprisingly little investigation of the predatory tactics used by araneophagic (spider-eating) insects. Here, we compare the pursuit tendency, outcome and predatory tactics of *S. bituberus* against five species of web-building spider. We found that *S. bituberus* were most likely to hunt and capture spiders from the genus *Achaearanea*, a particularly common prey in nature. Capture of *Achaearanea* sp. was more likely if the prey spider was relatively small, or if *S. bituberus* was in poor condition. *S. bituberus* used two distinct predatory tactics, 'stalking', in which they slowly approached the prey, and 'luring', in which they attracted spiders by manipulating the web to generate vibrations. Tactics were tailored to the prey species, with luring used more often against spiders from the genus *Achaearanea*, and stalking used more often against *Pholcus phalangioides*. The choice of hunting tactic used by *S. bituberus* may reduce the risk posed by the prey spider.

Keywords Predatory tactic · Luring · Stalking · Behavioural flexibility

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Introduction

Predators use a wide range of tactics to catch prey, from sit-and-wait tactics, where the predator waits for prey to approach (e.g., snakes such as *Gloydius shedaoensis* that ambush their prey; Shine and Sun 2003), to active tactics, where the predator approaches the prey (e.g., cougars, *Puma concolor*, that stalk and chase their prey; Husseman et al. 2003). While some predators will use one tactic against all, or most, of their prey (e.g., crab spiders that ambush pollinating insects on flowers, Morse 1981; Heiling et al. 2005), others may flexibly alternate between tactics according to the type of prey, the environment or circumstances during the hunt. Flexible use of predatory tactics has been observed in a wide variety of taxa, including mammals (e.g., harbour seals, *Phoca vitulina*; Bowen et al. 2002), birds (e.g., loggerhead shrikes, *Lanus ludovicianus*; Yosef and Grubb 1993), reptiles (e.g., snakes, *Natrix maura*; Patterson and Davies 1982), fish (e.g., brook charr, *Salvelinus fontinalis*; Grant and Noakes 1987) and spiders (e.g., the jumping spider *Portia fimbriata*; Jackson and Blest 1982; Jackson 1995). A predator that hunts dangerous prey may use specialised, prey-specific tactics. For example, whiptail lizards simply catch and eat harmless crickets, but vigorously shake and throw dangerous scorpion prey before eating it (O'Connell and Formanowicz 1998).

Spiders are dangerous prey to the insects that hunt them, as the spider is both prey and potential predator. Descriptions of the predatory tactics used by araneophagic ('spider-eating') insects are limited to only a few studies. Several species of parasitic wasp use the tactic of flying into spider webs, forcing the spiders to drop from their webs to the ground where they may be more easily captured (*Sceliphron caementarium* (Blackledge and Pickett 2000) and *Pison morosum* (Laing 1988)). *Chalybion caeruleum*, another parasitic wasp, uses aggressive mimicry to lure *Argiope* spiders within attacking range (Blackledge and Pickett 2000). However, these wasps have each only been observed using the one predatory tactic against their spider prey.

Stenolemus assassin bugs are also predators of web-building spiders. Whilst little is known of the predatory tactics used by *Stenolemus* species studied to date, they appear to have very narrow prey ranges. For example, *Stenolemus lanipes* has been reported hunting the tangle-web spider *Achaearanea tepidariorum* (Hodge 1984) and *Stenolemus edwardsii* has been reported to hunt spiderlings of the common house spider *Ixeuticus robustus* (*Badumna insignis*) although it will feed on other small spiders when these are unavailable (Hickman 1969). In sharp contrast to reports for these species, *Stenolemus bituberus* has a wide prey range, and uses two distinct predatory tactics, ‘stalking’ and ‘luring’ (Wignall and Taylor 2008). When stalking spiders, *S. bituberus* slowly approach the spider until within attacking range. When luring spiders, *S. bituberus* manipulate the silk of the webs, generating vibrations that attract the resident spider into range. We present in this paper one of the first studies of how alternative predatory tactics are used by an araneophagic insect while hunting different prey spiders.

Materials and methods

Stenolemus bituberus and prey spiders (juveniles and adults of both) were collected from trees and buildings on Macquarie University campus (Sydney, Australia), and when possible were returned after testing. Juvenile *S. bituberus* cannot fly and are unlikely to move far, if at all, from the location where they were collected. As we did not visit trees more than once during each instar, it is unlikely that individual *S. bituberus* were tested more than once within an instar, although some individuals may have been re-tested at later instars. The spider species we collected were *Achaearanea extridium* ($n=50$) and *Achaearanea* sp. ($n=52$) (Theridiidae), *Badumna longinqua* ($n=54$) (Desidae), *Pholcus phalangioides* ($n=50$) (Pholcidae) and a species belonging to an unidentified genus from the family Uloboridae ($n=53$). These spiders represent circa 90% of the genera that *S. bituberus* have been observed hunting in the field (Wignall and Taylor 2008).

Spiders were collected 2–5 days before testing, and were placed in wooden frames (200×200×30 mm) to build webs. Frames closely resembled those of Jackson et al. (2002). They had a removable clear acrylic screen at the front, to which spiders could not attach their web (removed for tests), and a wooden screen at the back. Frames were cleaned with a damp cloth between tests and were set up outdoors under shade to maintain natural light, temperature and humidity.

On the morning of each test, *S. bituberus* were collected from the field and photographed under standard magnification through an Olympus SZX12 microscope using a ProgResC10 digital camera and proprietary software (Jenoptik L.O.S., Germany). Pronotum length and abdomen width were measured from images using UTHSCSA ImageTool v3.00 software. Condition was defined as residuals from the regression of pronotum length on abdomen width (see Jakob et al. 1996; Taylor et al. 2000). The relative size of the spider was calculated as body length of the spider divided by the body length of *S. bituberus*.

All tests were started in either early morning (6–10 A.M.) or late afternoon (5–7 P.M.), the most active periods of *S. bituberus* in nature (A. Wignall, personal observations). We randomly assigned each individual *S. bituberus* to a spider species. To transfer *S. bituberus* to the frame, we carefully removed the piece of paper on which it stood from the maintenance vial and placed it on the base of the frame. Observations started once *S. bituberus* placed a tarsus on the frame. Tests were aborted if *S. bituberus* failed to begin hunting (i.e., failed to contact a silk thread with a tarsus or antenna) within 1 h.

We recorded the predatory behaviour of *S. bituberus* and the responses of the spiders. Tests ran until: (1) *S. bituberus* caught the spider; (2) the spider caught *S. bituberus*; (3) the spider ran away (i.e., left the frame) or (4) *S. bituberus* abandoned the hunt (i.e., left the frame or no activity for 90 min). For each hunt, we assessed whether the luring tactic was used or whether *S. bituberus* relied only on stalking. We report the p-values for whole models of statistical tests, then all subsequent p-values less than 0.1 for individual predictors.

Results

Stepwise logistic regression was used to investigate factors that might influence whether an *S. bituberus* initiated hunting. Factors initially included in the model were spider species, spider size (relative to assassin bug size) and *S. bituberus* condition (whole model chi-square 21.57, df=6, $p<0.01$). Of these, the only factor that significantly influenced pursuit tendency was spider species ($G_4=26.33$, $p<0.01$), with pairwise Fisher’s exact tests showing that *S. bituberus* were more likely to initiate hunts against *Achaearanea* sp. than against any other species ($p\leq0.05$ for all comparisons; Fig. 1a). *Stenolemus bituberus* were also more likely to initiate hunts against *A. extridium* and *P. phalangioides* than against Uloboridae sp. ($p<0.01$ for both comparisons).

We considered whether hunt outcome varied among the spider species hunted, excluding Uloboridae sp. for which all *S. bituberus* abandoned their hunts (Fig. 1b). Hunts had significantly different outcomes for different spider species

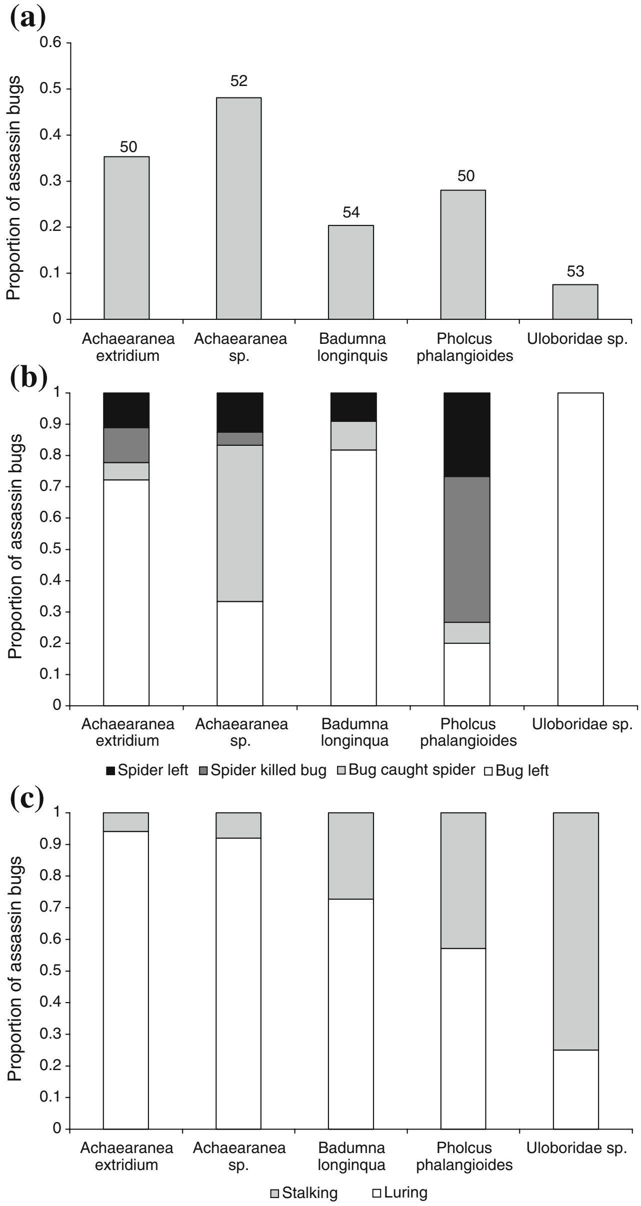

Fig. 1 For each spider species (sample sizes indicated above *bars*), **a** proportion of *S. bituberus* initiating hunts; **b** proportion of each of the four possible outcomes of a hunt; and **c** proportion of *S. bituberus* using either the luring or stalking tactic

(Fisher's exact test, test statistic=30.46, $p<0.01$). Pairwise Fisher's exact tests revealed all comparisons to be significant (all $p<0.05$) except for between *A. extridium* and *B. longinqua* ($p=0.89$; Fig. 1b). There was a strong tendency for *S. bituberus* to abandon hunts against *A. extridium*, *B. longinqua* and Uloboriidae sp., high probability of being killed in hunts against *P. phalangioides*, and high probability of success in hunts against *Achaearanea* sp. (Fig. 1b).

Stepwise logistic regression was used to assess the influence of spider species (excluding Uloboridae sp. due to small sample sizes), spider relative size and *S. bituberus'* condition on the predatory tactic adopted (whole model chi-square=12.63, df=6, $p=0.05$). Of these, only spider species influenced predatory tactic ($G_3=9.08$, $p=0.03$). Pairwise Fisher's exact tests showed that *S. bituberus* were more likely to use the luring tactic against *A. extridium* and *Achaearanea* sp. and more likely to rely on stalking alone against *P. phalangioides* (both $p<0.05$; Fig. 1c).

Stepwise polytomous logistic regression was used to analyse factors associated with the outcome of hunts against *Achaearanea* sp. The other spider species were excluded from this analysis as small sample sizes for some of the outcomes introduced instability in the models. Factors included in the model were spider relative size, *S. bituberus'* condition and the distance at which the hunt began (whole model chi-square=14.36, df=6, $p=0.03$). We found that *S. bituberus* were more likely to catch spiders rather than abandon the hunt if they were large relative to the spider ($G_3=8.70$, $p=0.03$) or if they were in poor condition ($G_3=8.25$, $p=0.04$) (Fig. 2). The probability of any of the four possible outcomes of the hunt was not affected by the tactic used (chi-square=0.86, df=3, $p=0.84$). The duration of successful hunts did not vary with the relative size of the spider or with *S. bituberus'* condition (whole model $F_{2,\ 16}=0.93$, $p=0.42$).

Discussion

The predatory behaviour of *S. bituberus* assassin bugs varied with prey spider species. In particular, hunts were initiated more often against *A. extridium* and *Achaearanea* sp. than against the other spider species. This is consistent with field observations indicating that spiders from the genus *Achaearanea* are among their main prey (Wignall and Taylor 2008). Other *Stenolemus* assassin bugs also prey on *Achaearanea* spiders, these being the sole reported prey of *S. lanipes* (Hodge 1984). *S. bituberus* appears to differ from other studied *Stenolemus* in preying on spiders and spiderlings from many different genera (and families), although it is possible that more detailed investigation would reveal wider prey ranges than those reported to date for other *Stenolemus* species.

S. bituberus select their predatory tactic according to spider species, with luring used more often against each of the *Achaearanea* species than against *P. phalangioides*. Prey-specificity of predatory tactic may be related to differences in aggressiveness of each spider species, and hence differences in the probability of counter-attack. Both *P. phalangioides* and spiders from the genus *Achaearanea* are known to throw silk at prey snared by their webs (Jackson et al. 1990; Hajer and Hrubá 2007). However, *P. phalangioides* are also web-invading aggressive mimics (Jackson and Brassington 1987) and we observed more individuals of this species counter-

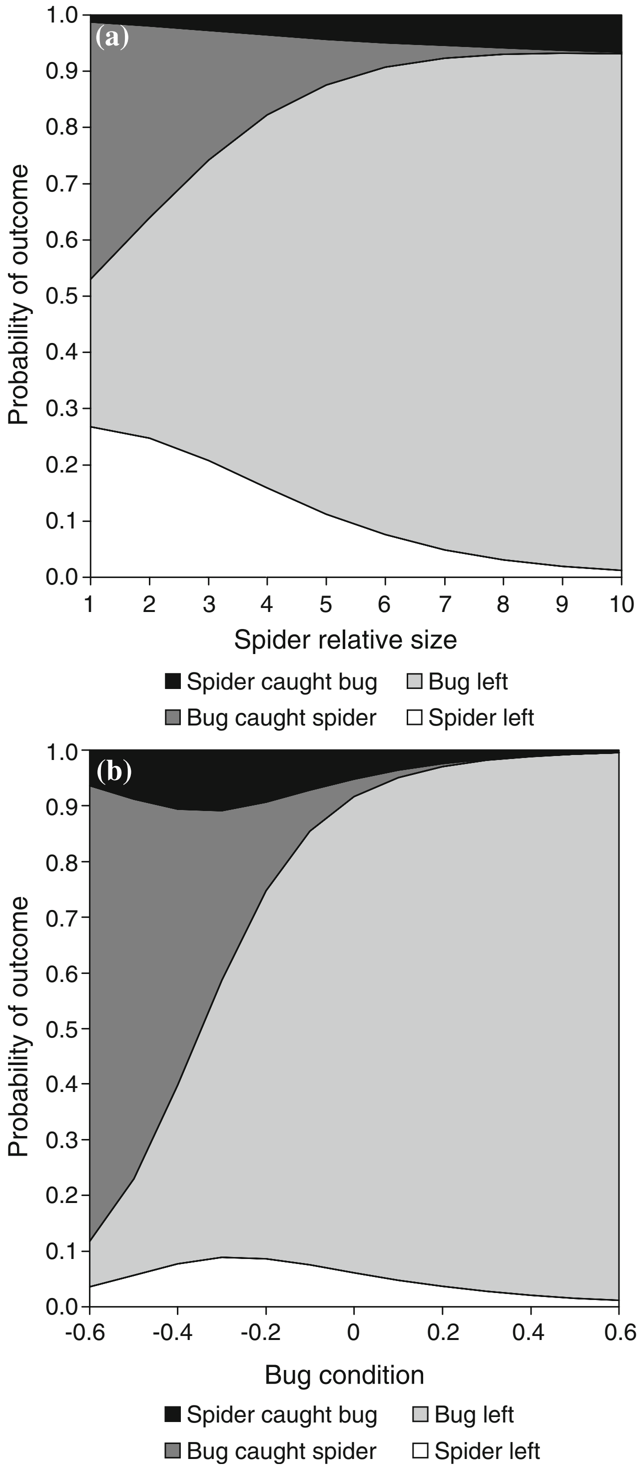

Fig. 2 Influence of **a** spider relative size (calculated as body length of the spider divided by the body length of *S. bituberus*) and **b** *S. bituberus*' condition (defined as the residuals from a regression of pronotum length on abdomen width) on the outcome of hunts of *Achaearanea* sp

attacking and killing *S. bituberus* than spiders from the genus *Achaearanea* (see Fig. 1b). In other studies, we have found *P. phalangioides* to be much more prone to rapidly approach and attack artificial vibratory stimuli compared with *Achaearanea* species (A. Wignall, unpublished data). Hence, *S. bituberus* may reduce the risk of detection and counter-attack by stalking rather than luring *P. phalangioides*. Alternatively, *S. bituberus* may be better able to attack the body of *P. phalangioides* when stalking. When luring *P. phalangioides*, attacking the body may be more difficult due to this species' long legs with which it can throw silk at the assassin bug from a distance. A still further hypothesis may be that *S. bituberus* alters predatory tactic, not to reduce risk, but to increase the probability of capturing the spider. However, we found no evidence to suggest that, for hunts against *Achaearanea* sp. at least, the predatory tactic affects capture rate.

Although the relative tendencies varied among prey species, *S. bituberus* did use both stalking and luring tactics against each spider species tested. Interestingly, neither spider size nor *S. bituberus*' condition influenced the tactic used. For example, prey size affects the risk posed by prey, and as a result the predatory tactic adopted, in *Nephila* orb-weaving spiders (Higgins 2007). However, while predatory tactic was not affected, *S. bituberus* did tend to abandon more hunts against larger spiders (see Fig. 2), indicating that spider size may still be a factor in the assessment of risk.

Generally, predators capture small prey more easily than large prey (e.g., Husseman et al. 2003). Indeed, predators are usually larger than their prey (e.g., Magalhães et al. 2005). In our experiments, *S. bituberus* were more likely to capture smaller *Achaearanea* sp. and were more likely to abandon hunts against larger spiders. These results suggest both that larger spiders are more dangerous and that *S. bituberus* can discern spider size, perhaps visually, chemically or using seismic cues transmitted through the web. Size-dependent risk of counter-attack on predators has been reported in several species, including a phytodsiid predator *Typhlodromus bambusae* whose nymphs are more vulnerable than adults to counter-attack from prey spider mites (*Schizotetranychus celarius*) (Saito 1986).

The condition of *S. bituberus* also influenced the outcome of hunts against *Achaearanea* sp. *Stenolemus bituberus* that were in poor condition were more likely to persist and capture the spider, whereas those that were in better condition were more likely to abandon the hunt (Fig. 2). Optimal foraging theory predicts that as the quality of the environment improves, predators become more selective of prey (e.g., Osenberg and Mittelbach 1989). *Stenolemus bituberus* with better body condition are likely to have been collected from better quality sites, and hence may be more selective of the spiders they persist in hunting. Alternatively, *S. bituberus* in poorer condition may be more likely to risk hunting dangerous prey, as has been observed in other species that will take risky prey when starved (e.g., Gillette et al. 2000).

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References

Blackledge TA, Pickett KM (2000) Predatory interactions between mud-dauber wasps (Hymenoptera, Specidae) and *Ariope* (Araneae, Aranediae) in captivity. J Arachnol 28:211–216

Bowen WD, Tully D, Boness DJ, Bulheier BM, Marshall GJ (2002) Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar Ecol Prog Ser 244:235–245

Gillette R, Huang R-C, Hatcher N, Moroz LL (2000) Cost-benefit analysis potential in feeding behavior of a predatory snail by integration of hunger, taste, and pain. Proc Nat Acad Sci 97:3585–3590

Grant JWA, Noakes DLG (1987) Movers and staters: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. J Anim Ecol 56:1001–1013

Hajer J, Hrubá L (2007) Wrap attack of the spider *Achaearanea tepidariorum* (Araneae: Theridiidae) by preying on mealybugs *Planococcus citri* (Homoptera: Pseudococcidae). J Ethol 25:9–20

Heiling AM, Chittka L, Cheng K, Herberstein ME (2005) Colouration in crab spiders: substrate choice and prey attraction. J Exp Biol 208:1785–1792

Hickman VV (1969) The biology of two emesine bugs (Hemiptera: Reduviidae) occurring on the nests or webs of spiders. J Entomol Soc Aust (N.S.W.) 6:3–18

Higgins L (2007) Juvenile *Nephila* (Araneae, Nephilidae) use various attack strategies for novel prey. J Arachnol 35:530–534

Hodge M (1984) Anti-predator behavior of *Achaearanea tepidariorum* (Theridiidae) towards *Stenolemus lanipes* (Reduviidae): preliminary observations. J Arachnol 12:369–370

Husseman JS, Murray DL, Power G, Mack C, Wenger CR, Quigley H (2003) Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591–601

Jackson RR (1995) Cues for web-invasion and aggressive mimicry signalling in *Portia* (Araneae, Salticidae). J Zool, Lond 236:131–149

Jackson RR, Blest AD (1982) The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilisation of webs and predatory versatility. J Zool Lond 196:255–293

Jackson RR, Brassington RJ (1987) The biology of *Pholcus phalangioides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. J Zool Lond 211:227–238

Jackson RR, Brassington RJ, Rowe RJ (1990) Anti-predator defences of *Pholcus phalangioides* (Araneae, Pholcidae), a web-building and web-invading spider. J Zool Lond 220:543–552

Jackson RR, Pollard SD, Cerveira AM (2002) Opportunistic use of cognitive smokescreens by araneophagic jumping spiders. Anim Cogn 5:147–157

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77:61–67

Laing DJ (1988) The prey and predation behaviour of the wasp *Pison morosum* (Hymenoptera: Sphecidae). New Zeal Entomol 11:37–42

Magalhães S, Janssen A, Montserrat M, Sabelis MW (2005) Prey attack and predators defend: counterattacking prey trigger parental care in predators. Proc Roy Soc Lond, B 272:1929–1933

Morse DH (1981) Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. Am Mid Nat 105:358–367

O’Connell DJ, Formanowicz DR Jr (1998) Differential handling of dangerous and non-dangerous prey by naïve and experienced Texas spotted whiptail lizards, *Cnemidophorus gularis*. J Herpet 32:75–79

Osenberg CW, Mittelbach GG (1989) Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. Ecol Monog 59:405–432

Patterson JW, Davies PMC (1982) Predatory behavior and temperature relations in the snake *Natrix maura*. Copeia 1982:472–474

Saito Y (1986) Prey kills predator: counter-attack success of a spider mite against its specific phytoseiid predator. Exp Appl Acarol 2:47–62

Shine R, Sun L-X (2003) Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper’s strike? Funct Ecol 17:340–348

Taylor PW, Hasson O, Clark DL (2000) Body postures and patterns as amplifiers of physical condition. Proc Roy Soc Lond, B 267:917–922

Wignall AE, Taylor PW (2008) Biology and life history of the araneophagic assassin bug *Stenolemus bituberus* including a morphometric analysis of the instars (Heteroptera, Reduviidae). J Nat Hist 42:59–76

Yosef R, Grubb Jr TC (1993) Effect of vegetation height on hunting behavior and diet of loggerhead shrikes. Condor 95:127–131