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## Are fleeing “noisy” lizards signalling to predators?

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**Abstract** Many prey signal to predators with the intention of deterring further pursuits. In the lizard *Psammodromus algirus*, individuals sometimes escape with noisy long runs on dry leaves, whereas on many other occasions they escape quietly and with short flights. We hypothesised that the duration of this noisy display might be considered as an auditory signal of their alertness and ability to escape directed to predators. We examined in the field the escape behaviour of the lizard *P. algirus* in response to a human observer acting as a predator and tested a series of predictions to analyse this hypothesis. During a noisy escape response, lizards escaped sooner and ran further and for a longer time, while passing potential refuges before hiding. Production of noise was not entirely dependent on environmental factors, such as temperature or microhabitat, and was not directed to warn conspecifics because most individuals were solitary. Lizards still made noise when concealed and in response to successive approaches, which might be interpreted as a signal of alertness to the predator approach. In addition, condition of individuals with noisy responses could be assessed from their ability to run further and for a longer time, and because, in contrast to quiet responses, speed and distance were not positively correlated with environmental temperature. Thus, they might be in a better condition or internal state because they were able to run at high speed under unfavourable conditions. We suggest that lizards with noisy escape responses might be honestly signalling their alertness and ability to escape to avoid being chased.

**Keywords** Antipredator behaviour · Escape behaviour · Lizards · *Psammodromus algirus* · Pursuit-deterrence signals

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### Introduction

Among the varied mechanisms of antipredator behaviour, many prey make signals directed to the potential predator (Hasson 1991; Caro 1995). According to the pursuit-deterrence hypothesis, some of these signals have the message that the prey is aware of the predator's presence and additionally may inform it about the escape potential of the prey (Fitzgibbon and Fanshawe 1989; Hasson 1991). In any case, the purpose is to signal that the probability of a successful attack has diminished and, thus, deter the pursuit. Alternatively, some of these signals have been interpreted as a way to warn kin or other conspecifics of the danger (Sherman 1977; Smith 1991), or to be a strategy to startle the predator (Edmunds 1974; Bildstein 1983), or simply as behaviours aimed to enhance the escape performance of the prey (Lingle 1993).

Signals directed to the predator with the probable function of deterring its pursuit have been described in mammals (Holley 1993; Caro 1994), birds (Woodland et al. 1980; Cresswell 1994), and fish (predator inspection behaviour; Godin and Davis 1995). Reptiles have a suite of antipredatory responses with many varied behavioural displays whose functions remain frequently unexplained (Greene 1988), and some of them might also be interpreted as deterrent signals directed to predators. However, few such signals have been described, exceptions being the tail displays of the iguanid lizards *Cophosaurus texanus* and *Callisaurus draconoides* (Dial 1986; Hasson et al. 1989), and the expansion of the throat fan (dew-lapping) of *Anolis cristatellus* (Leal 1999; Leal and Rodríguez-Robles 1995, 1997), which, apart from their social function, may also be used apparently to signal alertness to predators before the attack.

*Psammodromus algirus* is a medium-sized lacertid lizard inhabiting Mediterranean forests of the Iberian Peninsula and Northwest Africa. These lizards are important prey for many predators that rely on acoustic and visual cues such as some raptorial birds (e.g. *Buteo buteo* or *Falco tinnunculus*), shrikes (*Lanius excubitor*) (Martín and López 1990), and mammals such as weasels (*Mustela*

*nivalis*) or foxes (*Vulpes vulpes*), from which they escape by fleeing into the deep layer of leaf litter under cover of bushes (Martín and López 1995a). In this previous study, we described how individuals sometimes run to hide in refuges that are similar in quality but farther than the nearest available one. Because leaf litter is readily available in their habitat, a long run on dry leaves can be quite noisy, and, thus, the intensity and duration of this noisy display might be considered as an auditory signal directed towards predators. Moreover, individuals do not always escape with noise; very often they escape quietly and with short flights directly to the nearest refuge (Martín and López 1995a). This suggests that the costs and benefits of this behaviour differ among individuals or situations, which might reflect differences in their quality and/or internal state. The signal might have evolved because hiding under leaf litter is unsafe, and a concealed lizard could be easily captured if located again by the predator. Predator-deterrent signals can only be evolutionarily stable if they are honest and costly to the signaller, and if the cost is correlated with the signaller's quality (Zahavi 1977; Grafen 1990; Michod and Hasson 1990; Hasson 1994). We hypothesise that individual *P. algirus* lizards that run for longer and make more noise, which presumably is more costly, might be honestly signalling to predators their alertness and ability to escape, thereby deterring further pursuits. Predators might have learned that individual lizards that escape with more noise are also more difficult to capture. Thus, predators may divert the attack to other individuals that do not signal, avoiding the costs of a probably unsuccessful pursuit.

In this article, we examined the escape response of *P. algirus* lizards in the field in response to a human observer acting as a predator. We tested a series of predictions to analyse whether noisy escape responses might be interpreted as a signal directed towards the predator, and whether this signal could honestly inform the predator about their condition and ability to escape. We additionally tested predictions to analyse whether, alternatively, noisy escape might be interpreted as a way to startle predators, a signal to warn conspecifics, or simply as a result of external conditions, such as temperature or microhabitat, independent of lizards' behaviour (see Caro 1986; Hasson et al. 1989; Caro et al. 1996 for similar approaches).

## Materials and methods

### Study area

The observations were conducted during spring (April–May) 1996 in an oak forest near Cercedilla (40°44'N, 4°02'W, Madrid province, Spain). Vegetation includes primarily trees and low sapling bushes of the deciduous oak (*Quercus pyrenaica*), as well as less-abundant and dispersed perennial bushes of *Cistus laurifolius*, and *Rosa* sp. Oak leaf litter is very abundant on the ground all year around, and especially during spring when the oak leaves are shed. Population densities of *P. algirus* in this area are highly positively correlated with the amount of low shrubs and leaf litter (Díaz and Carrascal 1991).

### Escape behaviour

We walked through the area until a lizard was sighted with binoculars, whereupon we attempted to approach the lizard directly. The same person performed all approaches, walked at the same medium speed, and wore the same clothing, while another person recorded the lizard's behaviour, to avoid confounding effects that may affect risk perception of lizards (e.g. Burger and Gochfeld 1993; Cooper 1997b). The usual response of the lizard was to flee rapidly to the protective cover of a bush and hide in the leaf litter under it (Martín and López 1995a). We defined "approach distance" as the distance between the lizard and the observer when the lizard first moved (straight-line measured to the nearest 0.1 m). We characterised the response magnitude by measuring the total distance covered during active flight ("escape trajectory distance"). The trajectory was estimated by memory and measured after the lizard hid. The "flight distance" was defined as the straight line distance from the lizard's initial position to hiding. The "resultant distance" was calculated as the straight line distance from the observer to the final refuge (Ba-uwens and Thoen 1981; Snell et al. 1988; Bulova 1994; Cooper 1997a). "Escape duration" was the duration of the active flight, measured with a stopwatch during the escape response. Thereafter, we could calculate also the "escape speed" (escape trajectory distance divided by the time taken).

Production of noise during the escape response was evaluated through previous experience with the escape responses of this lizard, as being "quiet" (no or very little sound) or "noisy" (much more noise than expected for a small lizard running away). These two categories were normally distinct for an experienced observer. However, any sequences that could not be assigned clearly to one category were discarded.

The escape response of lizards may be determined by the microhabitat and availability of refuges (Martín and López 1995a; Cooper 1997a), which affect the costs and benefits of fleeing (Ydenberg and Dill 1986). Thus, we measured to the nearest 0.1 m the "distance to the nearest refuge" (patch of abundant leaf litter under cover of low bushes, like those in which the lizards hide). Because the presence of the observer might constrain the lizard's escape direction, we also measured the "distance to the nearest potential refuge available in the direction of the escape trajectory". Microhabitats at the origin of the lizard's flight were recorded and classified according to their safety against predators as "safe" (patches of leaf litter under shrubs) or "unsafe" (open areas with grass or bare soil). We also noted whether the refuge was clearly visible from the observer's position or was obscured by bushes, rocks, and so forth. The latter refuges were defined as "visual refuges" that were assumed to minimise the probability of being located by a predator. To analyse the microhabitat along the escape trajectory, we used a scored stick standing vertically and recorded at 50 cm intervals the contacts with the stick at substrate level of grass, leaf litter, bare soil, or rocks and, when it was presented, the type of bush vegetation cover (*Quercus*, *Cistus*, or *Rosa*) at each point. We also noted if the point could be used as a potential refuge by lizards. This procedure allowed us to calculate the value of eight habitat variables: number of contacts (i.e. cover) with each substrate and vegetation type, and the number of potential refuges along the escape trajectory (Scheibe 1987; Martín and López 1998).

The escape response is influenced by temperature in some lizards (Rand 1964; Hertz et al. 1982). Lizards could not be captured immediately after they fled to measure their body temperatures. However, air temperature is a relevant environmental variable for thermoregulation in *P. algirus* (Carrascal and Díaz 1989). Thus, to control for temperature affecting our results, we measured the air temperature with a digital thermometer to the nearest 0.1°C (shaded bulb, 2 cm above the sighting point), immediately after each escape sequence.

### Data analysis

Only adult individuals were included in the analyses. Given the large size of the surveyed area (more than 5 km<sup>2</sup>), the high density of lizards (about 60 adults/ha, unpublished data), and our avoidance of presampling areas already surveyed, we consider the prob-

ability of repeatedly measuring the same individual as very low. We therefore treat all measurements as independent data. Differences between noisy and quiet escape responses were evaluated by means of analyses of variance (ANOVA) on data normalised by logarithmic transformation. Tests of homogeneity of variances (Hartley's  $F_{\max}$  test) showed that in all cases variances were not significantly heterogeneous (Sokal and Rohlf 1995).

## Results

### Characteristics of the escape responses

Forty five out of 149 escape responses (30.2%) were noisy. Lizards with a noisy escape response typically fled at high speed, running and jumping over leaf litter for a long time and passing by potential refuges before finally hiding. In a noisy escape response lizards fled at significantly greater approach distances, had significantly greater flight and escape trajectory distances as well as flight time, and achieved significantly greater resultant distances than those that escaped quietly (Table 1). In contrast, average escape speeds of lizards during a noisy or quiet response were similar.

### Is the type of escape response dependent on external factors?

The production of noise might be determined simply by the presence or absence of leaf litter on the substrate, although the proportion of substrate points with leaf litter along the escape trajectory was very high in most of the observations (data pooled: mean $\pm$ SE=63.5 $\pm$ 2.4%, range=10–100%). However, noisy and quiet responses occur through microhabitats with a similar proportion of leaf litter (noisy: 60.5 $\pm$ 5.0%; quiet: 51.4 $\pm$ 3.4%;  $F_{1,147}=2.45$ ,  $P=0.12$ ). Thus, some lizards were able to run over leaf litter without making a lot of noise. For example, even when the proportion of leaf litter was greater than 50%, most individuals (61.5% of 91) still made a relatively quiet response.

Air temperatures determine lizards' body temperatures, and speed is higher at optimal temperatures. Thus, when temperature is optimal, lizards might run farther and

faster, making more noise. However, noisy responses occurred at air temperatures that were not significantly different from temperatures when quiet responses occurred (noisy: 19.0 $\pm$ 0.5°C; quiet: 19.4 $\pm$ 0.4°C;  $F_{1,147}=0.18$ ,  $P=0.67$ ).

### Are lizards signalling to conspecifics?

If noisy lizards intended to warn other individuals, then they should make more noise, or make noise more frequently, in the presence of conspecifics. However, individual lizards were rarely found with another conspecific. Most of the lizards that escaped with either a quiet (92.3%) or a noisy response (86.7%) were solitary. Moreover, the frequency of noisy responses of lizards found in pairs (35.7% of 14) was not different from that of solitary individuals (28.9% of 135;  $\chi^2_1=0.35$ ,  $P=0.55$ ).

### Does noise enhance crypticity, startle the predator, or indicate prey alertness?

If noise enhances the crypticity of lizards and contributes to startling the predator, lizards with noisy responses should, in addition, use refuges that are out of view of the predator ("visual refuges", see Methods), because otherwise, the noise would help the predator to locate the refuge. By the same token, lizards with noisy responses should escape through microhabitats with more cover that would make it harder for the predator to locate the lizard. In a noisy response, lizards hid more frequently in "visual refuges" (86.7% of 45) than in a quiet response (58.6% of 104;  $\chi^2_1=14.55$ ,  $P=0.00014$ ). In contrast, the proportion of vegetation cover in the microhabitats that lizards escaped through was not significantly different between quiet (44.9 $\pm$ 3.0%) and noisy responses (48.8 $\pm$ 4.0%;  $F_{1,147}=0.52$ ,  $P=0.48$ ).

The flash concealment hypothesis (Bildstein 1983) predicts that if noise functions to cause predators to lose eye contact with their prey, noise disappearance should be quick and unexpected when the lizard hides under the leaf litter. Noise should, thus, be produced when they escape but not after they are already hidden, because this would

**Table 1** Characteristics of the quiet and noisy escape responses of *P. algirus* lizards. Numbers are means ( $\pm$ 1 SE).  $F$  and  $P$  values from one-way ANOVAs on response type are given

|                                   | Quiet<br>( $n=104$ ) | Noisy<br>( $n=45$ ) | $F$   | $P$    |
|-----------------------------------|----------------------|---------------------|-------|--------|
| Escape distances (m)              |                      |                     |       |        |
| Approach                          | 2.44 $\pm$ 0.10      | 3.10 $\pm$ 0.18     | 10.53 | 0.0015 |
| Escape trajectory                 | 1.65 $\pm$ 0.14      | 2.54 $\pm$ 0.31     | 9.74  | 0.002  |
| Flight                            | 1.40 $\pm$ 0.11      | 2.10 $\pm$ 0.25     | 9.40  | 0.003  |
| Resultant                         | 3.20 $\pm$ 0.13      | 4.39 $\pm$ 0.28     | 15.10 | 0.0002 |
| Escape duration (s)               | 1.12 $\pm$ 0.09      | 1.61 $\pm$ 0.16     | 9.24  | 0.003  |
| Escape speed (m/s)                | 1.72 $\pm$ 0.10      | 1.74 $\pm$ 0.14     | 0.08  | 0.78   |
| Distance to available refuges (m) |                      |                     |       |        |
| Nearest                           | 0.47 $\pm$ 0.05      | 0.38 $\pm$ 0.07     | 1.20  | 0.28   |
| In the escape trajectory          | 0.59 $\pm$ 0.06      | 0.60 $\pm$ 0.11     | 0.56  | 0.46   |

indicate to the predator the location of the refuge. Our observations, however, indicated that, during a noisy response, most of the lizards (84.4% of 45) still made noise while concealed under the leaf litter, and, if approached again, they did not remain quiet. Instead they made sudden short movements concealed in the leaf litter with a lot of noise in response to our successive approaches.

If noisy escape responses indicate that lizards have detected the predator, then lizards should make noise preferentially in relaxed situations when the risk of being captured is lower, for example, when they can escape at longer approach distances from the predator, or only in microhabitats with more cover. Approach distances of lizards in noisy responses were greater than those of quiet responses (Table 1). This result might arise only from the safety at the initial location of the lizard (i.e. lizards in unsafe microhabitats would escape earlier during the interaction with the predator than those in safe microhabitats). However, the proportion of noisy responses in unsafe microhabitats (57.8% of 45) was not significantly different from that of quiet responses (67.3% of 104;  $\chi^2_1=1.87$ ,  $P=0.17$ ). Additionally, lizards with noisy responses were not significantly farther from the nearest available refuge or from the nearest refuge found in the direction of the escape trajectory than lizards with quiet responses (Table 1). Also, lizards that started to flee at greater approach distances were not significantly farther from the final refuge used (correlation between approach and flight trajectory distances; quiet:  $r=0.03$ ,  $P=0.76$ ; noisy:  $r=-0.13$ ,  $P=0.39$ ).

#### Can lizard condition be assessed from noise?

Predator-deterrent signals can only be evolutionarily stable if they are honest and costly to the signaller, and if the cost is correlated with the signaller's quality or state. When considering the average escape speed, lizards did not run faster during a noisy response than during a quiet one (see Table 1). However, noisy responses might be energetically more costly because they were of longer duration, and consequently escape speed was maintained for longer. Thus, lizards that escape with a noisy response might decrease the energy available for subsequent flights if the predator continues the pursuit. Another possible cost of fleeing with noise is attracting a predator's attention or enabling it to follow the prey easily. During a noisy response, lizards started to flee much earlier than during a quiet response. This may possibly draw the attention of an otherwise unaware predator, which may result in the predator chasing that individual. In addition, by running for a long time lizards increased their exposure to predators by failing to use potential refuges (number of refuges in escape trajectory; noisy:  $9.6\pm 0.9$ ; quiet:  $6.0\pm 0.3$ ;  $F_{1,147}=17.51$ ,  $P<0.0001$ ).

Temperature may have a strong influence on sprint speed of lizards. Thus, escape speed in the quiet responses was significantly correlated with air temperature ( $r=0.46$ ,  $P<0.0001$ ,  $n=74$ ). In contrast, and although air

temperatures did not differ between responses (see above), speed was not dependent on air temperature in the noisy responses ( $r=0.05$ ,  $P=0.74$ ,  $n=42$ ). Moreover, the escape trajectory distance of the quiet responses was also significantly correlated with air temperature ( $r=0.40$ ,  $P=0.03$ ), whereas in the noisy responses, escape distance was not significantly correlated with air temperature ( $r=0.05$ ,  $P=0.80$ ).

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## Discussion

The results of our analysis indicate that noise production is not directly dependent on environmental factors, such as air temperature or microhabitat. For example, individuals were also able to run over abundant leaf litter without much noise. Moreover, our observations suggest that lizards detected us well enough in advance of when they decided to escape, because their heads were often turned towards the approaching observer, and thus, most lizards would probably be able to escape and hide without calling predators' attention. Nevertheless, some of them escaped with enough noise to call our attention, and, thus, presumably also that of potential predators. Our data show that "noisy" flight responses seem to be due to some characteristics of individual lizards, not of their environment.

Noise is clearly not aimed at warning kin or other conspecifics in *P. algirus* lizards, because most noisy individuals were solitary. This is also expected for a species that lacks any type of parental care, and in which individuals are not grouped socially (Hirth and McCulloch 1977). The only exception is males that guard females during the mating season, but we found no evidence that males escaped with noise to attract the predator and allow the female to escape unnoticed. Moreover, we also observed escaping with noise for females, young males that did not guard females, and adult individuals outside of the mating season.

Many lizards escape from predators by running to hide in the nearest available refuge (Greene 1988; Cooper 1997a). This is a safe and inexpensive tactic if the predator cannot capture the lizard once it is in the refuge. However, hiding under leaf litter is not entirely safe, because the predator could locate the refuge and capture a concealed lizard. One crucial point for *P. algirus* lizards may be to hide in a spot that is difficult to locate. Thus, *P. algirus* lizards do not hide in the nearest refuge but run farther, and noise may help prevent the predator from predicting the position of the lizard when it finally hides. However, noise may also attract the attention of a predator, which may chase the noisy lizard, while passing other, quieter individuals. Alternatively, our data cannot refute that certain individuals were more frightened by our approach; they therefore fled sooner, ran farther, and paid less attention to the substrate over which they ran while creating more noise. These individuals might have been less familiar with their present habitat (Clarke et al. 1983) or be of "shy" rather than "bold" phenotypes (Wilson et al. 1994). However, our observa-

tions indicate that many lizards with a noisy escape response still made noise when concealed under leaf litter, and they made more noise in response to our successive approaches. This behaviour seems contradictory to a cryptic or “shy” strategy and is contrary to the predictions of the flash concealment hypothesis (Bildstein 1983); thus, it might rather be interpreted as a signal of alertness to the predator approach.

Our results suggest that the condition of *P. algirus* lizards might be inferred from their ability to run farther and for a long time. The intensity and duration of the noise produced by the flight might, thus, be an honest indicator of endurance and ability to run and escape. We have classified the escape responses as being noisy or quiet. However, noises might be of different intensities that are probably related to flight characteristics. This would allow experienced predators a more precise assessment of a lizard’s ability to run and escape. Temperature has a strong influence on a lizard’s sprint speed (Bennet 1980; Van Berkum 1986). However, noisy lizards ran faster and farther independently of temperature and, thus, might be in a better physical condition that allowed them to run at the same level of speed even when temperature was unfavourable. Alternatively, these individuals might already have attained an optimal body temperature, and an associated optimal running performance, whereas individuals with suboptimal body temperature might escape with quiet responses. In any case, the absence of noise would indicate that the ability to run of that particular individual is not optimal either permanently, due to its worse physical condition, or temporarily, due to its current internal state (i.e. low body temperature). Also, rattling in rattlesnakes (*Crotalus viridis*) provides reliable cues to size and body temperature, and this information seems to be used by ground squirrels (*Spermophilus beecheyi*) to assess the dangerousness of the approaching snake (Rowe and Owings 1996). Similarly in the leopard lizard (*Gambelia wislizenii*), vocalisation is joined with an aggressive defence, and this behaviour is temperature dependent (Crowley and Pietruszka 1983).

Alternatively, quiet responses might not be related to an individual’s condition, but to situations in which production of noise would not be necessary to elude the predator. For example, lizards very close to a safe refuge, such as a rock crevice, may need only a short run, without noise, to be safely hidden, thus, avoiding the costs of a long noisy response. Escape responses of *P. algirus* are also of shorter duration in safer microhabitats with more cover (Martín and López 1995a). However, more cryptic and shorter escape responses are also typical of lizards with impaired locomotion, such as pregnant females (Bauwens and Thoen 1981; Schwarzkopf and Shine 1992; Braña 1993) or small juveniles (Martín and López 1995b).

The behaviour of noisy *P. algirus* lizards could be compared to stotting in ungulates (Caro 1986, 1994). Stots and noisy displays are both performed during flight sequences in response to a predator approach. Variation in the rate and duration of stotting or noise could allow

predators to assess the ability of potential prey to escape if the performance is closely related to the prey’s ability to outrun a predator (Fitzgibbon and Fanshawe 1989). We suggest that “noisy” escape responses of *P. algirus* lizards might have evolved firstly as a way to startle predators. Noise may enhance the effect of confusion of a lizard running through a habitat with high density of low bushes and abundant leaf litter. However, we also suggest that, because noise can be related to lizard characteristics, predators using this information would save time and energy wasted on predictably unsuccessful chases. Lizards would thus benefit by avoiding being chased if signalling their alertness and ability to escape before the attack. The system could be evolutionary stable because only lizards in good condition or good internal state would signal at a high level, and therefore noise would be an honest signal of condition (Zahavi 1977; Grafen 1990; Vega-Redondo and Hasson 1993). Further experiments are clearly needed to analyse whether natural predators are able to use this information when deciding whether to pursue a lizard or avoid the chase.

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## References

- Bauwens D, Thoen C (1981) Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J Anim Ecol* 50:733–743
- Bennet AF (1980) The thermal dependence of lizard behaviour. *Anim Behav* 28:752–762
- Bildstein KL (1983) Why white-tailed deer flag their tails. *Am Nat* 121:709–715
- Braña F (1993) Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66: 216–222
- Bulova SJ (1994) Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. *Copeia* 1994:980–992
- Burger J, Gochfeld M (1993) The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. *J Herpetol* 27:426–430
- Caro TM (1986) The function of stotting in Thomson’s gazelles: some tests of the predictions. *Anim Behav* 34:663–684
- Caro TM (1994) Ungulate antipredator behaviour: preliminary and comparative data from African bovines. *Behaviour* 128: 189–228
- Caro TM (1995) Pursuit-deterrence revisited. *Trends Ecol Evol* 10:500–503
- Caro TM, Lombardo L, Goldizen AW, Kelly M (1996) Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. *Behav Ecol* 6:442–450
- Carrascal LM, Díaz JA (1989) Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammotromus algirus*. *Holarct Ecol* 12:137–143
- Clarke MF, Burke Da Silva K, Lair H, Pocklington R, Kramer DL, McLaughlin RL (1983) Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. *Oikos* 66: 533–537
- Cooper WE Jr (1997a) Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can J Zool* 75:943–947

- Cooper WE Jr (1997b) Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia* 1997:613–619
- Cresswell W (1994) Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviours of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behav Ecol Sociobiol* 34:217–223
- Crowley SR, Pietruszka RD (1983) Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): the influence of temperature. *Anim Behav* 31:1055–1060
- Dial BE (1986) Tail display in two species of iguanid lizards: a test of the "predator signal" hypothesis. *Am Nat* 127:103–111
- Díaz JA, Carrascal LM (1991) Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. *J Biogeogr* 18:291–297
- Edmunds M (1974) Defense in animals: a survey of anti-predator defenses. Longman, New York
- FitzGibbon CD, Fanshawe J (1989) Stotting in Thomson's gazelles: an honest signal of condition. *Behav Ecol Sociobiol* 23:69–74
- Godin J-GJ, Davis SA (1995) Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proc R Soc Lond B* 259:193–200
- Grafan A (1990) Biological signals as handicaps. *J Theor Biol* 144:517–546
- Greene HW (1988) Antipredator mechanisms in reptiles. In: Gans C, Huey RB (eds) *Biology of the reptilia*, vol 16. Wiley, New York, pp 1–152
- Hasson O (1991) Pursuit-deterrence signals: communication between prey and predators. *Trends Ecol Evol* 6:325–329
- Hasson O (1994) Cheating signals. *J Theor Biol* 167:223–238
- Hasson O, Hibbard R, Ceballos G (1989) The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can J Zool* 67:1203–1209
- Hertz E, Huey RB, Nevo E (1982) Fight versus flight: body temperature influences defensive responses of lizards. *Anim Behav* 30:676–679
- Hirth DH, McCullough DR (1977) Evolution of alarm signals in ungulates with special reference to white-tailed deer. *Am Nat* 111:31–42
- Holley AJF (1993) Do brown hares signal to foxes? *Ethology* 94:21–30
- Leal M (1999) Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Anim Behav* 58: 521–526
- Leal M, Rodríguez-Robles JA (1995) Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* 1995:155–161
- Leal M, Rodríguez-Robles JA (1997) Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim Behav* 54:1147–1154
- Lingle S (1993) Escape gaits of white-tailed deer, mule deer and their hybrids: body configuration, biomechanics and function. *Can J Zool* 71:708–724
- Martín J, López P (1990) Amphibians and reptiles as prey of birds in southwestern Europe. *Smithsonian Herp Inf Serv* 82: 1–43
- Martín J, López P (1995a) Influence of habitat structure on escape tactics of *Psammotromus algirus* lizards. *Can J Zool* 73: 129–132
- Martín J, López P (1995b) Escape behaviour of juvenile *Psammotromus algirus* lizards: constraint of or compensation for limitations in body size? *Behaviour* 132:181–192
- Martín J, López P (1998) Shifts in microhabitat use by the lizard *Psammotromus algirus*: responses to seasonal changes in vegetation structure. *Copeia* 1998:780–786
- Michod RE, Hasson O (1990) On the evolution of reliable indicators of fitness. *Am Nat* 135:788–808
- Rand AS (1964) Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* 45:863–864
- Rowe MP, Owings DH (1996) Probing, assessment and management during interactions between ground squirrels (Rodentia: Sciuridae) and rattlesnakes (Squamata: Viperidae). 2: Cues afforded by rattlesnake rattling. *Ethology* 102:856–874
- Scheibe J (1987) Climate, competition, and the structure of temperate zone lizard communities. *Ecology* 68:1424–1436
- Schwarzkopf L, Shine R (1992) Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behav Ecol Sociobiol* 31:17–25
- Sherman W (1977) Nepotism and the evolution of alarm calls. *Science* 197:1246–1253
- Smith WP (1991) Ontogeny and adaptiveness of tail-flagging behavior in white-tailed deer. *Am Nat* 138:190–200
- Snell HL, Jennings RD, Snell HM, Harcourt S (1988) Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol Ecol* 2:353–369
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Van Berkum FH (1986) Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40: 595–604
- Vega-Redondo F, Hasson O (1993) A game-theoretic model of predator-prey signaling. *J Theor Biol* 162:309–319
- Wilson DS, Clark AB, Coleman K, Dearstyne T (1994) Shyness and boldness in humans and other animals. *Trends Ecol Evol* 9:442–446
- Woodland DJ, Jaafar Z, Knight ML (1980) The 'pursuit-deterrent' function of alarm signals. *Am Nat* 115:748–753
- Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. *Adv Study Behav* 16:229–249
- Zahavi A (1977) Reliability of communication systems and the evolution of altruism. In: Stonehouse B, Perrins CM (eds) *Evolutionary ecology*. MacMillan, London, pp 253–259