Number, Speeds, and Approach Paths of Predators Affect Escape Behavior by the Balearic Lizard, *Podarcis lilfordi*

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ABSTRACT.—The number of simultaneously attacking simulated predators and their approach speeds and angles affected escape trajectories and flight initiation distance in Balearic Lizards (*Podarcis lilfordi*). Our findings confirmed predictions prey flee in directions maximizing distance from predator(s). During slow approaches, escape angle was 45° when approached by two predators at right angles and 90° when approached from opposite directions. Escape at close to 45° by lizards approached at slower speed by a single predator supports the hypothesis that prey use escape trajectories allowing them to visually monitor predators. Flight angles were closer to being straight away from a predator during faster approaches, suggesting that distance maximization may be more important than monitoring predator position when risk is great. When predators approached from opposite directions, flight angle shifted away from the faster predator, suggesting that lizards may have equalized risk from both predators based on positions and speeds. Flight initiation distance was greater for approach by predators side by side than by one only during faster approaches, suggesting that risk is a joint function of predator number and speed. Flight initiation distance was greater when predators approached at right angles than side by side, perhaps because of difficulty of monitoring multiple predators in different locations. Distance fled did not differ among treatments and may have been affected by distance to refuge. Thus, Balearic Lizards adjusted flight initiation distance and escape trajectories in ways that enhanced their abilities to avoid predation during simultaneous approaches by two predators.

Escape during brief predator-prey encounters has been studied intensely in the past decade, and much of this research has been guided by a graphical model (Ydenberg and Dill, 1986) that predicts how closely a prey should allow a predator to approach before fleeing and duration of stays in refuge (extension by Martín and López, 1999). Most of our knowledge about escape is limited to flight initiation distance (distance between predator and prey when escape begins = approach distance; e.g., reviews by Lima and Dill, 1990; Stankowich and Blumstein, 2005) in response to a single predator and time of emergence from refuges after escaping. However, prey may be confronted by multiple risk factors simultaneously (e.g., Smith and Belk, 2001; Cooper et al., 2003a,b). In at least one avian species, flight initiation distance is greater during approach by two predators than by one (Geist et al., 2005). Effects of simultaneous attack by multiple predators are beyond the scope of current models of escape behavior.

Escaping prey must select flight initiation distance, initial escape direction (flight angle),

and possibly a refuge. If the predator continues to approach and remains nearby, prey may alter course and decide how far to flee (escape distance = distance fled) and whether to enter refuge. Relatively few studies have investigated factors affecting flight angle (e.g., Dill, 1974; Hall et al., 1986; Domenici, 2002) and distance fled (e.g., Cooper and Pérez-Mellado, 2004; Smith and Lemos-Espinal, 2005).

For prey that escape without entering a refuge or for which many refuges are available, initial flight angles may be selected to maximize distance between predator and prey during escape (Domenici and Blake, 1993; Domenici, 2002). As a single predator approaches, prey can stay farthest from it by moving directly away, but Domenici and Blake (1993) observed two peak escape trajectories in fish, one directly away, and one at an angle of 50° to directly away. They suggested that the peaks reflect maximizing distance between predator and prey and keeping the predator in view (Hall et al., 1986).

Prey may select among available refuges by taking into account their distances, relative security, and flight angle relative to the predator. The initial flight angle might be a compro-

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mise between movement directly away, movement keeping the predator in view, and movement toward a safer site. In species that consistently flee into or toward refuges, flight angle is determined largely by the direction to the refuge (Cooper, 1997a).

Distance fled may be determined by balancing risk and cost in a manner formally identical to Ydenberg and Dill's (1986) economic model of flight initiation distance (Cooper et al., 2006). This is suggested by variation of distance fled with degrees of both risk and cost. Risk factors affecting distance fled include predator approach speed (Martín and López, 1996), predator persistence (Cooper, 1997a), distance of prey from refuge (Cooper, 1997b), degree of cover (Snell et al., 1988; Martín and López, 1995), and predation pressure (Stone et al., 1994). The cost of losing feeding opportunities reduces distance fled (Cooper and Pérez-Mellado, 2004; Cooper et al., 2006). Distance fled by Balearic Lizards (*Podarcis lilfordi*) decreases as number of food items they must abandon to flee increases, suggesting a trade-off between predation risk and cost of escape (Cooper and Pérez-Mellado, 2004; Blumstein and Pelletier, 2005; Cooper et al., 2006).

Prey may encounter multiple predators sequentially or simultaneously. They employ strategies to avoid encounters with multiple predators that are likely to be encountered sequentially because they occupy different microhabitats (e.g., Krupa and Sih, 1998; Hopper, 2001; Amo et al., 2004; Stapley, 2004), but much less is known about effects of simultaneously attacking predators on escape decisions. Because multiple attackers, including social hunters, may approach from different angles, their angles of approach relative to each other may affect flight angles. Because predation risk may be greater from multiple than single attackers, flight initiation distance is predicted to be greater during attacks by two predators than by a single predator. This prediction was verified for one of two bird species (Geist et al., 2005). Distance fled might not be greater during approach by multiple predators in prey that escape to refuge or if prey flee just far enough to reestablish a margin of safety.

We test the hypothesis that Balearic Lizards begin to escape in the direction that maximizes distance between them and approaching predators. In recording escape directions, we considered movements right or left of the predator's approach path to be equivalent, reducing the 360° directional scale to a 180° axial scale (Fig. 1). For one predator or two approaching side by side, the predicted flight angle is 0° with respect to the approach path. If two similar predators approach at right angles
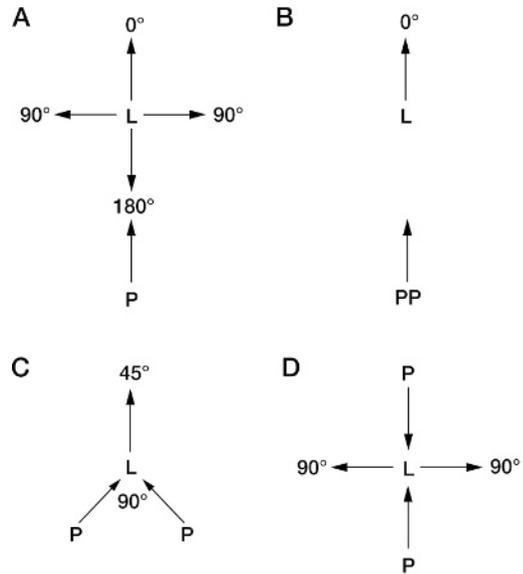
FIG. 1. Scale of escape direction and predicted flight angles. (A) Escape directly away from the predator's path is 0°, directly toward the predator is 180°, and at right angles to either side is 90°. Predicted flight angle for a lizard (B) is 0° when two predators approach side-by-side, (C) 45° with respect to each predator when two predators approach from right angles, and (D) 90° when two predators approach from opposite directions.

at the same speed, predicted flight angle is 45° with respect to each predator. When two comparable predators approach from opposite directions, the predicted flight angle is 90°. These angles would keep prey equidistant from the two predators.

Although Balearic Lizards are presumably rarely attacked by socially hunting predators, they may occasionally encounter multiple predators. More generally, they may be exposed to multiple risks simultaneously (e.g., Smith and Belk, 2001; Cooper et al., 2003a,b) and, therefore, subject to natural selection favoring ability to make escape decisions minimizing overall risk.

The predictions are for prey in a uniform habitat that does not use refuges. If prey sometimes use refuges and multiple refuge sites are available, as in the present study, other flight angles might decrease risk more. Mean flight angle >0° is predicted when prey flee toward refuges. Because a more rapidly approaching predator poses greater threat at a given distance and is more likely to overtake a prey on a given flight path before it reaches refuge, flight angle is expected to be closer to predicted values during faster than slower approaches. When two predators approach from opposite directions at different speeds,

the flight angle is predicted to be closer to zero for the faster predator.

MATERIALS AND METHODS

Balearic Lizards are abundant on islets near Menorca, Balearic Islands, Spain. We observed escape by adults on a plot of >1 ha on the islet of Aire where these small omnivorous lizards attain unusually high population density (up to 20,000/ha; Pérez-Mellado, 1998). The habitat contains many bushes and rock crevices used as refuges. We did fieldwork in May 2005 on sunny days when lizards were fully active.

We examined effects of simultaneous attack by two predators by having two human investigators act as simulated predators. Ability by researchers to communicate intentions, rapidly position ourselves appropriately in the field, and execute simultaneous approaches greatly facilitated data collection. Substituting humans for natural predators raises two potential problems. First, prey might not perceive investigators as predators. Natural predators of Balearic Lizards include birds, especially Kestrels (*Falco tinnunculus*). Mammals, such as feral cats (*Felis domesticus*) and genets (*Genetta genetta*), are believed to be responsible for extinction of *Podarcis lilfordi* on Menorca (Pérez-Mellado et al., 1997). Human beings are larger than typical predators on Balearic Lizards, but *P. lilfordi* and other lizards respond to approaching human beings by attempting to escape (e.g., Cooper, 1997a, 1999, 2000; Cooper et al., 2004) and by using refuges (Martín and López, 1999; Cooper et al., 2003a; Martín et al., 2003) in ways predicted by escape theory. Thus, lizards react as if approaching investigators pose a threat although they might react differently, perhaps more strongly, when attacked by natural predators.

A second possible pitfall is that investigators know the type of trial being conducted. Because of this knowledge, we used standardized methods of approach to eliminate possible bias. We practiced approach speeds to ensure consistency. Before conducting trials, investigators practiced slower (80.8 ± 0.8 m/min, these and other data are $\bar{x}$ ± 1.0 SE) and faster (115.6 ± 1.6 m/min) approaches 10 times, attaining consistency for each speed. We practiced approaching from different directions relative to each other to ensure consistency.

To begin a trial, we located a stationary lizard positioned where investigators could approach continuously and directly while affording the lizard clear views of both investigators. We included only individuals having intact tails because reduction in running speed after autotomy (Cooper et al., 2004) might affect escape strategies. Investigators moved to positions appropriate to category of approach for the trial, each starting the trial at 11–14 m from the lizard. When both investigators had adopted the starting position and signaled readiness, they simultaneously approached the lizard at a preselected speed.

When a lizard fled, each investigator stopped and recorded (1) flight initiation distance, (2) distance fled (before the lizard stopped running and was stationary for at least one second), and (3) flight angle. Flight angle was designated as initial escape trajectory with respect to the predator's approach path. We did not record initial lizard orientation, but lizards turned to flee in a selected direction rather than fleeing in the direction of orientation. If we pursued lizards, some fled directly into refuge and others changed directions during escape (unpubl. obs.). Because we stopped moving when escape began, they fled relatively short distances along a single flight path without substantial changes in angle. Distances were recorded to the nearest 0.1 m. We made no distinction between escapes to left or right, such that possible flight angles are limited to 0–180°. No data were collected for two predators approaching rapidly at 180°. We estimated flight angle visually with 4.5 ± 0.81° error based on ability to estimate measured angles.

Four types of approaches were made at the slower speed: a single predator (N = 12), two predators approaching the lizard side by side (0° relative to each other, N = 12), two predators approaching the lizard on paths separated by 90° (N = 10), and two predators approaching the lizard from opposite directions (180°, N = 8). Other types of approaches were made with one predator approaching at the faster speed, two predators at the faster speed approaching side by side or at right angles, and two predators approaching from opposite directions, one at the slower and one at the faster speed (N = 12 each). We did not record data for distance fled in two trials: one for two predators approaching side by side at the slower speed; the other for two predators approaching from opposite directions at different speeds. We conducted the trials at various locations and tried to avoid testing each individual more than once. Because Balearic Lizards are mobile, active foragers (pers. obs.) and individuals were not marked, it is possible that some individuals might have been tested more than once. However, given the extremely high density of lizards, the potential for pseudoreplication was very low.

Data analyzed were flight initiation distance (for the closer of two predators when approach speed differed), distance fled, and flight angle.
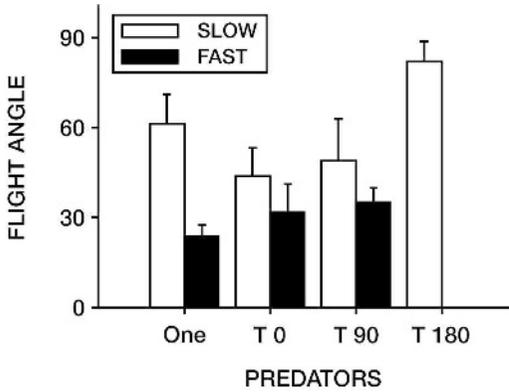
Fig. 2. Flight angles (degrees) by *Podarcis lilfordi* varied with speed and directions of approach by predators. One, single predator; T 0, two predators approached side by side; T 90, two predators approached separated by 90°; T 180, two predators approached from opposite directions (180°). No data were collected for predators approaching rapidly at 180°. Error bars represent 1 ± SE.

When flight angles could differ between investigators, the angle was taken with respect to the same investigator (DH) for all trials in which both investigators approached at the same speed or for the faster investigator when approach speed differed. Raw data were examined to ensure that assumptions of parametric analyses for normality (Kolmogorov-Smirnov or Shapiro-Wilks tests) and homogeneity of variance (Levene's tests) were met. Data on flight initiation distance and distance fled were logarithmically transformed as needed to remove significant departures from normality and heterogeneity of variance prior to analysis of variance. Multiple comparisons were made using Duncan's tests (Zar, 1996). Differences in flight angle were analyzed using circular statistics (Watson-Williams tests) for axial data (collapsed to 180°; Sokal and Rohlf, 1995). Tests were two-tailed unless stated otherwise, with $\alpha = 0.05$. When multiple tests were conducted by methods not accounting for experiment-wide error, raw probabilities are given, but significance is reported using sequential Bonferroni adjustment for number of tests (Wright, 1992).

RESULTS

Flight angle.—With one predator, approach speed significantly affected flight angle ($F = 10.92$; df = 1,22; $P = 0.003$; Fig. 2), which was greater at the slower speed, indicating escape on a path closer to directly away from the predator at faster approach speed. Variance was greater for slower approaches (Levene's $F_{1,22} = 15.10$, $P < 0.001$). When two predators approached at

right angles, flight angles did not differ significantly between approach speeds (Fig. 2; $F_{1,18} = 0.46$, $P > 0.10$). Flight angle was $48 \pm 9°$ for slower approaches and for faster approaches was $35 \pm 5°$ for one predator and $55 \pm 5°$ for the other. For side-by-side approaches, flight angle did not differ significantly between approach speeds (Fig. 2; $F_{1,22} = 1.94$, $P > 0.10$).

For approaches from opposite directions, flight angle was significantly closer to 90° (Fig. 2; $F_{1,20} = 22.94$, $P = 0.00011$) when both predators approached at slower speed than when speeds differed. Flight angle for the faster predator was much smaller ($32.9 \pm 9.4°$). Six of 12 individuals fled at angles within 10° of directly away from the faster predator; nine of 10 fled in the range 70–90° when both predators approached at the slower speed. At the slower approach speed, flight angles varied with differences in angles of approach (Fig. 2). When two predators approached at either 0° or 90°, flight angles were close to 45°. This is greater than expected for approaches at 0° but matches the theoretical expectation for equal avoidance of both predators approaching at 90°. Flight angle did not differ significantly between approaches by two predators side by side and by a single predator at the slower approach speed (Fig. 2; $F_{1,22} = 1.40$, $P > 0.10$). When predators approached from opposite directions at slower speed, flight angle was within 85–95° for all but one lizard, which fled at 30° and 60° with respect to the two predators.

Flight angle was significantly smaller (Fig. 2; $F_{1,20} = 10.60$, $P = 0.004$) when two predators approached at 0° than 180° and was marginally smaller ($F_{1,16} = 3.92$, $P = 0.032$, one-tailed) for two predators approaching at 90° than 180°. Flight angles did not differ significantly between 0° and 90° approaches ($F_{1,18} = 0.02$, $P > 0.10$).

Flight initiation distance and distance fled.—At slower approach speed (four treatments), the distribution of flight initiation distance did not differ from normality (Shapiro-Wilks statistic = 0.97, df = 43, $P > 0.10$) or homogeneity of variance ($F_{3,40} = 0.43$, $P > 0.10$), but distance fled was significantly nonnormal (Shapiro-Wilks statistic = 0.90; df = 43; $P = 0.01$). Logarithmically transformed distance fled met the assumptions of normality and homogeneity of variance ($F_{3,38} = 0.35$; $P > 0.10$). Flight initiation distance (Fig. 3) did not differ among groups ($F_{3,40} = 1.60$, $P > 0.10$); neither did the transformed distance fled (Table 1; $F_{3,38} = 1.74$, $P > 0.10$).

When approaches at the faster speed were added to the analysis (slower and faster speeds for one predator, two predators approaching side by side, and two predators approaching at
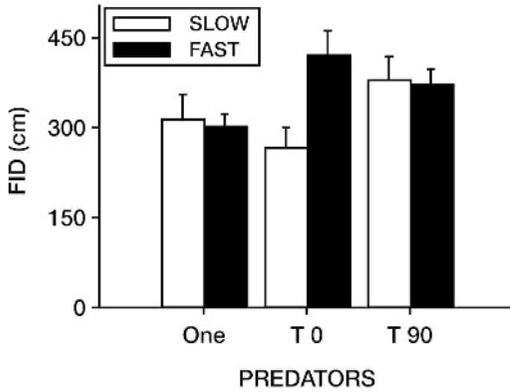
FIG. 3. Flight initiation distance by *Podarcis lilfordi* approached at slower and faster speeds. One, single predator; T 0, two predators approached side by side (0°); T 90, two predators approached at right angles (90°). Error bars represent 1 ± SE.

right angles), flight initiation distance met the assumptions of normality (Kolmogorov-Smirnov $d = 0.063$; $P > 0.10$) and homogeneity of variance ($F_{5,64} = 1.76$, $P > 0.10$). Neither of the main effects was significant (Fig. 3; approach speed: $F_{1,64} = 2.38$, $P < 0.13$; approach type: $F_{2,64} = 1.84$, $P < 0.17$), but interaction between approach speed and approach type was significant ($F_{2,64} = 4.02$, $P < 0.023$; Fig. 3). Mean flight initiation distances were very similar and did not differ significantly ($P > 0.10$ each) for fast and slow approaches by one predator or by two predators approaching at right angles. Mean flight initiation distance was significantly greater at the faster approach speed when two predators approached side by side ($P < 0.006$). Additional simple effects differed significantly: flight initiation distance at the slower approach speed was significantly shorter when the predators approached side by side than at right angles ($P < 0.04$) and marginally shorter than when predators approached at right angles at the faster speed $P < 0.056$). For the faster speed, flight initiation distance was significantly greater for two predators side by side than for one predator ($P < 0.029$).

When the analysis is limited to the four groups in which one or two (side by side) predators approached directly at the slower or faster speed, the main effect of approach speed is not quite significant ($F_{1,44} = 3.97$, $P < 0.053$), the main effect of number of predators is not significant ($F_{1,44} = 1.03$, $P > 0.10$), and the interaction is significant ($F_{1,44} = 5.89$, $P < 0.02$; Fig. 3). Duncan's tests show that flight initiation distance is significantly greater for two predators approaching side by side at the faster speed than in the other three groups (one predator, slower: $P < 0.04$; two predators, slower: $P < 0.0055$; one predator, faster: $P < 0.025$).

Distance fled for the six groups in the previous two paragraphs (Table 1) departed from normality significantly (Kolmogorov-Smirnov $d = 0.177$, $P < 0.01$) for raw, but not for logarithmically transformed, data (Kolmogorov-Smirnov $d = 0.097$, $P > 0.05$). Variances of transformed data were homogeneous ($F_{5,62} = 1.06$, $P > 0.10$). No effects were significant (approach speed: $F_{1,62} = 1.19$, $P > 0.10$; approach type: $F_{2,62} = 0.17$, $P > 0.10$; interaction: $F_{2,62} = 0.17$, $P > 0.10$; Table 1).

DISCUSSION

Flight angle.—Initial escape directions confirmed several, but not all, predictions based on maximization of distance between predator(s) and prey during escape. The flight angle for approaches by a single predator and for two predators approaching side by side were <90° as predicted, but close to 45°, much greater than the 0° predicted for escape directly away. When approach speeds do not require escape at full speed immediately, flight angles >0° (i.e., not directly away) might be preferable because they permit monitoring predator position and movements during escape. Findings are consistent with the proposal by Hall et al. (1986) that fish escape on trajectories that allow them to keep the predator in the visual field and are nearly identical with Domenici and Blake's (1993) peak

TABLE 1. Distance fled (cm) by *Podarcis lilfordi* for types of approaches. Zero distance fled indicates immediate refuge entry.

| Approach type | Approach speed | | | | | | | |
| | Slower | | | | Faster | | | |
	Mean	SE	Range	N	Mean	SE	Range	N
One predator	57.5	9.5	20–120	12	49.2	9.5	10–120	12
Two predators at 0°	59.1	9.8	25–140	11	46.4	4.3	20–70	12
Two predators at 90°	52.5	10.2	0–130	12	48.8	7.3	20–100	12
Two predators at 180°	40.4	7.0	10–80	12				

escape trajectory explained by keeping the predator in view.

Escape trajectories might have been influenced also by direction, distance, and security of nearby refuges. Refuges presumably were equally available in all directions over the course of the study, and for each lizard, multiple nearby refuges were available, offering a wide range of possible directions for escape toward refuge. Thus, lizards could select refuges while still selecting escape trajectories to maximize distance from the predator or allow monitoring the predator during escape. Refuge selection is unlikely to have strongly affected the mean escape angle but may have increased its variability.

For prey approached by two predators at the same speed, variation in flight angle with approach angles supports the hypothesis that the prey minimized risk by maximizing their distance from both predators during escape. When two predators approached from opposite directions, the prediction that prey should flee at right angles to both predators was strongly confirmed. The prediction was also supported for two predators approaching at right angles, for which the flight angle was very close to $45°$ for slow approaches and did not differ significantly between fast and slow approaches.

For faster approaches by a single predator, the smaller flight angle indicates escape almost directly away, verifying the prediction for maximization of distance between predator and prey. At slower approach speed, the greater flight angle and higher variability may indicate that the lizards were vigilant during escape, keeping the single predator in view (Hall et al., 1986; Domenici and Blake, 1993). Furthermore, the longer time available to assess risks and reach refuges may have allowed lizards to select from a wider range of escape paths. At the greater approach speed, avoiding capture by fleeing away as rapidly as possible may initially outweigh other considerations.

Deflection away from the more dangerous of two predators accounts for a smaller flight angle for the faster predator. Lizard trajectories kept them further from the faster predator than escape at right angles to both predators would have. Approach speed strongly affects flight initiation distance in lizards (e.g., Cooper, 1997c, 2003a,b; Smith, 1997). Our results show that it also influences escape trajectories.

Flight angle in this study is the initial direction taken by a prey. Because the predators stopped moving when escape began, lizards did not need to adjust escape trajectories during pursuit and continued on relatively straight paths until stopping. More complex escape behaviors occur in some species, including

erratic, unpredictable changes in direction, tight turns, and other changes in direction during pursuit (Edmunds, 1974), and some theoretical predictions have been made about changing escape trajectories during pursuit (Weihs and Webb, 1984). Further research on these topics is needed to understand the pursuit phase of predator-prey encounters. Future studies of flight angle should attempt to unravel conditions maximizing distance from predators versus monitoring them and relationships between these and refuge use.

Flight initiation distance and distance fled.— Flight initiation distance was affected by presence of two predators only at the greater approach speed, as indicated best by factorial analysis for one and two directly approaching predators at two speeds. When two predators approached side by side, flight initiation distance was greater at the faster speed and greater than for a single predator at either speed. Interaction between approach speed and number of predators indicates that number of predators affected flight initiation distance as predicted at the faster speed. The difference between speeds in effect of two predators on flight initiation distance can potentially explain interspecific differences such as that observed by Geist et al. (2005). Different species could have different thresholds of approach speed for number of predators to affect flight initiation distance.

Flight initiation distance increases with degree of risk for factors such as approach speed and directness and the prey's distance from refuge, although not all species exhibit some of these relationships (e.g., Martín and López, 1995; Cooper, 2003a; Smith, 1997; Stankowich and Blumstein, 2005). Prey were expected to assess risk as greater when two predators were present. Either they assessed predators approaching side by side at the slower speed as posing little or no greater risk than a single predator, or the finding is a novel contradiction of economically based escape decisions (Ydenberg and Dill, 1986). Lizards fled as if two faster predators were more dangerous than one, perhaps because less time was available to select an escape path and fewer escape routes were feasible because of wider angle subtended by two predators.

The greater flight initiation distance for two predators approaching at right angles than side by side suggests that the lizards assessed greater risk during the former. This assessment may be attributable to difficulty of monitoring two predators in different locations simultaneously or to greater limitation in escape options. In Crimson Rosellas (*Platycerus elegans*), flight initiation distance was greater during

approaches by two predators than by one but did not differ for predators approaching side by side versus one behind the other (Geist et al., 2005). Similarity of flight initiation distances by these birds in the two treatments is consistent with both monitoring and escape limitation hypotheses.

Flight initiation distance increased at greater approach speed in previous studies of lizards using single predators (e.g., Cooper, 1997a, 2003a,b; Smith, 1997) but did not in this study. Two factors probably account for this anomalous finding. First, the difference between the slower and faster approach speeds was smaller than in other studies. Second, because flight initiation distance decreases as distance to refuge decreases, proximity to refuges decreases the difference in predicted flight initiation distance for slowly and rapidly approaching predators. As lizards were close to multiple refuges, a small difference in approach speed was presumably not great enough to cause a detectable difference in flight initiation distance. Nevertheless, our unpublished data show that flight initiation distance increases as approach speed increased in *P. lilfordi*.

Because distance to refuge affects distance fled (Cooper, 1997b), similarity of distance fled among treatments may be caused by proximity to multiple refuges. Most individuals did not enter refuges, but variation in distance to refuge might have masked effects of numbers and behavior of predators. Distance fled might also be unaffected if the lizards flee just far enough to maintain some margin of safety regardless of risk level.

Multiple predators.—Predation avoidance strategies are influenced by presence of different predators in different microhabitats (e.g., Soluk and Collins, 1988; Downes and Shine, 1998; Sih et al., 1998; Amo et al., 2004). Our data show that multiple predators and their behavior affect escape even in a species that may only rarely encounter more than one predator at a time. Being hunted by cooperative foragers may favor selection countering social hunting tactics, improving escape ability during simultaneous attacks. Even species depredated exclusively by solitary hunters may encounter more than one predator or other source of risk at once. Balearic Lizards and other species (e.g., Geist et al., 2005) make escape decisions minimizing risk from multiple predators. This ability may be a consequence of natural selection specifically to escape from multiple predators, but might also have evolved as part of a more general ability to respond to multiple simultaneous aspects of predation risk (Smith and Belk, 2001; Cooper et al., 2003a,b).

Because it is affected by a balance of risk and benefits obtainable by not fleeing, we predict that distance fled increases with number of predators if additional predators increases predation risk. However, risk does not always increase when multiple predators of different species are present (e.g., Kotler et al., 1992; Krupa and Sih, 1998) and in some circumstances might not do so when multiple predators of a single species are present. Distance fled is expected to increase with number of predators only if (1) prey do not flee into or adjacent to the nearest refuge and (2) risk increases with predator number.

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