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When hiding from predators is costly: Optimization of refuge use in lizards

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Abstract. Prey often respond to predators by increasing their use of refuges but relatively few studies have analyzed how prey decide when to resume their behavior after a predator's unsuccessful attack. This is important because refuge use may have some costs that should be minimized such as the loss of time available for foraging or mate searching. In addition, unfavorable conditions in refuges (e.g., suboptimal temperatures) might entail physiological costs such as hypothermia. Under these circumstances, animals should optimize the decision of when to come out from a refuge by balancing the fitness effects of the diminution of predation risk with time against the costs of loss of time available for other activities and loss of time spent at optimal body temperature. I review several experiments with lizards that support that individuals decide to come out from a refuge when the costs of hiding exceed predation risk in the exterior, and that there is an optimal emergence time. Optimization of these antipredatory behavioral strategies might help lizards to cope with changes in predation risk without incurring excessive costs.

Key words: predation risk, refuge use, antipredator behavior, lizards

Resumen. Muchas presas responden a los depredadores con un incremento en el uso de refugios, pero raramente se ha analizado cómo se decide cuándo salir del refugio para reanudar el comportamiento normal. Esto es importante porque el uso de refugios puede tener costes que deben ser minimizados. Entre los costes se encuentran, por ejemplo, la pérdida de tiempo y oportunidades para buscar alimento o parejas. Además, si el refugio tiene condiciones desfavorables (por ej. temperaturas bajas) puede haber costes fisiológicos como la hipotermia. En estas circunstancias, un animal debería optimizar su decisión de cuándo salir del refugio, teniendo en cuenta el beneficio de la disminución del riesgo de depredación con el tiempo, y los costes de la pérdida de tiempo disponible para otras actividades y el tiempo pasado a temperaturas desfavorables. Los resultados de varios experimentos demuestran que un saurio sale del refugio cuando los costes de uso del refugio son mayores que el riesgo de depredación en el exterior, y que existe un tiempo óptimo de emergencia. La optimización de estas estrategias comportamentales antidepredatorias podría ayudar a los reptiles a hacer frente a cambios en la presión de los depredadores sin caer en costes excesivos.

Introduction

Animals should optimize their antipredatory responses by balancing antipredator demands with other requirements (Sih, 1980; Pitcher et al., 1988; Lima & Dill, 1990). Thus, many prey are able to optimize their foraging behavior according to levels of predation risk (Lima & Dill, 1990; Lima, 1998). Moreover, even when predatory attack is imminent, some prey adjust their escape response to minimize the costs of flight (Ydenberg & Dill, 1986).

Numerous studies have shown that prey often respond to predator presence by increasing their use of refuges (Werner et al., 1983; Kotler, 1984; Sih, 1986; Sih et al., 1992), but relatively few studies have analyzed how prey decide when to resume their behavior after a predator's unsuccessful attack (Pitcher et al., 1988, Sih et al., 1988, Sih, 1992, 1997; Dill & Fraser, 1997). This is important because refuge use may have some costs that should be minimized such as, for example, the loss of time available for foraging (Godin & Sproul, 1988; Koivula et al., 1995; Dill & Fraser, 1997) or mate searching (Sih et al., 1990; Crowley et al., 1991). In addition, unfavorable conditions in refuges (e.g., suboptimal temperatures or oxygen levels) might entail physiological costs, such as hypothermia or hypoxia (Wolf & Kramer, 1987; Weatherhead & Robertson, 1992; Martín & López, 1999a). Cost of refuge use may influence the patterns of prey use of refuges, and this should have important effects on the predator-prey interaction (Sih, 1987; Ruxton, 1995) and, consequently, on the structure of the community (Orians, 2000).

Reptiles, and particularly lizards, suffer a high predation pressure (Martín & López, 1990, 1996), and many lizards escape from predators by fleeing into refuges (Greene, 1988; Martín & López, 1995, 2000a). However, because lizards are ectotherms, this simple antipredatory strategy may affect the time available for other activities and important physiological costs. Thus, lizards are an excellent model to study whether animals are able to compensate simultaneously predation risk and costs of refuge use. In this paper I will review several recent studies that suggest that lizards are able to optimize refuge use in relation to other ecological requirements. This can be accomplished mainly through behavioral modifications of time spent in refuges and by adjusting escape decisions which require that lizards being sensitive and responding appropriately to levels of predation risk and to short term fluctuations of ecological conditions.

Costs of refuge use

In ectothermic reptiles the attainment and maintenance of an optimal body temperature is essential to maximjze numerous physiological processes (Huey, 1982) and behaviors with important future fitness consequences (e.g. sprint speed and foraging efficiency; Bennett, 1980; Avery et al., 1982). Careful behavioral thermoregulation increases the time that lizards spend at physiologically favorable body temperatures (Bauwens et al., 1996). However, effective thermoregulation requires that appropriate sources of heat from solar radiation and/or warm substrates are available (Huey, 1982). Limitations of the thermal environment may frequently prevent reptiles from achieving preferred body temperatures. Behavioral thermoregulation increases growth rate by increasing time available for voluntary food intake (Avery, 1984; Autumm & De Nardo, 1995). Besides, the selection of elevated body temperatures following feeding (Tossini et al., 1994) may increase both digestive rate and efficiency (e.g. Harwood, 1979). Therefore, when reptiles are prevented from attaining their selected body temperatures, the excess of energy stored as fat in the fat body and liver should decrease and they should display reduced growth rates (Sinervo & Adolph, 1994). This is important because the amount of stored fat affects survival and future reproductive success of lizards (Ballinger, 1977).

By experimentally increased the frequency of attacks by a simulated predator (human) toward a group of wall lizards, *Podarcis muralis*, we examined the hypothesis that lizards may respond to an increase in risk of predation with an increase in refuge use, but that this strategy entail costs to their body condition (Martín & López, 1999b). The use of refuges placed in microhabitats of low quality for foraging and for attaining preferred body temperatures entails costs that were reflected in the body condition of individuals. At the end of the experimental period, experimental lizards increased the time spent into a refuge after an attack (recovery time), but they had significantly lower relative body mass than control individuals. An increase in the time spent into refuges at unfavorable temperatures during the experiment might lead to a loss of time available for foraging and a diminution of the efficiency of physiological functions, which resulted in loss of mass.

Thermal requirements and refuge use

Available, or safer, refuges may be in microhabitats with shady and colder conditions, such as rock crevices. The body temperature of a lizard that has retreated into a cool refuge will decrease below preferred levels after a period of time. This is especially important for small lizards, with low thermal inertia, because it could result in temperature impairment in only a few minutes. Lizards should minimize time spent in a refuge, especially when refuge thermal conditions are unfavorable relative to external ones. Costs will be higher when differences between external and internal thermal conditions are greater. Therefore, after an unsuccessful attack of a predator, an ectothermic prey should optimize the decision of when to come out from a refuge by balancing the fitness effects of the diminution of predation risk with time against the costs of loss of time available for other activities and loss of time spent at optimal body temperature.

The model of Ydenberg & Dill (1986) describes the trade-off between risk and cost for a prey fleeing to a refuge. A special case of this model predicts how emergence time from the refuge in lizards or other ectotherms should vary as a function of risk of predation and thermal costs of refuge use (Martín & López, 1999a). The analyses of the variation in emergence time from a refuge of the Iberian rock-lizard (*Lacerta monticola*) in the field under two different predation risk levels supported the predictions of the model. As predicted, time spent in the refuge was longer when the threat of the initial attack had been higher, and therefore the subsequent diminution of risk was lower. In addition, the effects of thermal costs were more relevant in the high risk situation. Time spent in the refuge under high risk increased when thermal conditions of the refuge were more similar to thermal conditions outside (i.e., physiological costs of refuge use were lower). These data suggest that optimization of refuge use strategies might help lizards to cope with changes in predation risk without incurring excessive physiological costs.

Foraging requirements and refuge use

The loss of foraging opportunities may be one of the main costs of refuges, because safer microhabitats (i.e. refuges) are also frequently the poorest in terms of their foraging profitability (Lima & Dill, 1990; Martín & Salvador, 1993a). With respect to foraging requirements, emergence times from a refuge should vary as a function of nutritional state of the prey and availability of food in the exterior, which affect directly to the magnitude of the costs of refuge use. Some studies of barnacles, birds and fishes have analyzed how the emergence time of prey is affected by its nutritional state (Dill & Gillet, 1991; Koivula et al., 1995; Krause et al., 1998). For example, the relative weight loss of individual fish was strongly correlated with a reduction in hiding time (Krause et al., 1998), and the duration of hiding of hungry willow tits was shorter than that of satiated ones (Koivula et al., 1995). In contrast to expectations, tubeworms, *Serpula vermicularis,* that experienced lower food levels, and were presumably hungrier, stayed in hiding longer (Dill & Fraser, 1997). Some prey seem also able to respond appropriately to short term fluctuations in food levels. Thus, tubeworms based their hiding behavior on current feeding conditions, rather than on average long-term conditions (Dill & Fraser, 1997). Some experiments have shown that lizards may alter several aspects of feeding behavior when predation risk increases (Martín & Salvador, 1993a; Martín & Avery, 1997; Cooper, 2000), suggesting that may exist a trade-off between predation risk and foraging. Thus, other field study tested whether emergence times from a refuge of the lizard *L. monticola* vary as a function of expected foraging opportunities and level of satiation of the lizard (Martín, López & Cooper, unpublished data). As predicted, short term fluctuations in availability of food influenced emergence times; when a lizard had just detected some food in the recent past, emergence times decreased greatly, because the loss of opportunities for foraging increased costs of refuge use. Furthermore, the characteristics and success of the encounter with food, nutritional state of lizards, and the added possibility of capturing new food items influenced the duration of hiding times. Therefore, foraging requirements and avoidance of predators may be conflicting demands that *L. monticola* lizards may optimize by modifying the duration of time spent in refuges.

Repeated attacks and multiple decisions

In some circumstances, prey may suffer successive repeated attacks in a short time. For example, many sit-and-wait predators may remain waiting for an individual prey outside the refuge and try a new attack. Alternatively, if predator density increases, the probability of an attack by a different individual predator also can increase. In these circumstances, a prey may consider that successive attacks may represent an increase in the risk of predation, but the costs of refuge use also may increase with time spent in the refuge. Thus, prey should make multiple related decisions on when to emerge from the refuge after each new attack.

We simulated in the field repeated predatory attacks to the same individuals of the lizard *L. monticola* and specifically examined the variation in successive emergence times from a refuge under different thermal conditions (i.e., different costs of refuge use) (Martín & López, 2001). The results of this experiment showed that risk of predation but also thermal costs of refuge use affected the duration of successive emergence times from the refuge in *L. monticola*. Initially, an increase in the frequency of predatory attacks was probably interpreted as an increase in the probability of a new attack (i.e., diminution of predation risk with time is slower). Thus, when costs of refuge use were low, lizards tended to increase the duration of successive emergence times to compensate the increase in predation risk. This result agrees with the general tendency of many animals, including lizards, which modify their microhabitat or refuge use according to the estimated levels of predation risk (Lima & Dill, 1990; Sih et al., 1992; Martín & Salvador, 1992, 1993b). In other experiment, the skink *Eumeces laticeps* also remained in refuges longer after the second of two successive similar approaches than after the first (Cooper, 1998). These data may indicate that lizards perceived a higher predation risk due to persistence by an individual predator, although individual recognition of the predator may not be needed if the assessment was just based on attack rate (Cooper, 1998). However, when the costs of refuge use increased, lizards tended to maintain or even to decrease the duration of successive emergence times, in spite of the increase in predation risk.

Escape decisions and costs of refuge use

Theoretical models of antipredator escape behavior suggest that prey might adjust their escape response such that the optimal approach distance would be the point where the costs of staying exceed the cost of fleeing (Ydenberg & Dill, 1986). Predation risk has been generally considered in the context of probability of mortality in the immediate future, however antipredatory decisions should be made based on consequences for long-term expected fitness (Clark, 1994). Thus, the escape decision should not only be dependent upon the potential benefit to be gained (i.e., risk reduction), but also on the reduction of posterior costs that can have important future fitness consequences. The latter include energetic cost of fleeing, lost opportunity costs for feeding (Bellman & Krasne, 1983; Stamp & Bowers, 1988), and risk of mortality consequent upon the use of a particular escape tactic (Dill et al., 1990). Antipredatory decisions should be made based also on consequences for long-term expected fitness, such as the costs of refuge use. For example, in lizards, the maintenance of an optimal body temperature is essential to maximize physiological processes (Huey, 1982). However, if unfavorable thermal conditions of refuges can decrease lizards' body temperature, their escape decision should be influenced by refuge conditions. The analyses of the variation in approach distances and emergence time from a refuge of the lizard *L. monticola* under two different predation risk levels and their relationship with the thermal environment supported these predictions (Martín & López, 2000b). When risk increased, lizards had longer emergence times, and thus costs of refuge use increased (a greater loss of time and body temperature). In a low risk situation, lizards that were farther from the refuge had longer approach distances, whereas thermal conditions were less important. However, when risk increased, lizards had longer approach distances when refuges were farther, but also when the external heating rate and the refuge cooling rate were lower. This suggests that in addition to the risk of predation, expected long-term fitness costs of refuges can also affect escape decisions.

Are refuges always safe?

Many prey live in communities that typically have multiple predators, which sometimes may have risk-enhancing effects, causing higher predation rates than expected. The mechanism that is usually thought to generate risk enhancement involves conflicting predator-specific prey defenses (Sih et al., 1998). Prey defenses against one predator may put at greater risk of being killed by the other predator. Some types of refuges may be only useful against some particular type of predators or may expose prey to other types of predators. For example, the mortality of a mayfly prey in the presence of both fish and stoneflies was greater than expected, because stoneflies caused mayflies to come out of hiding under rocks, thus resulting in greater exposure to fish (Soluk, 1993). Therefore, one of the costs of refuges used against one type of predator may be the exposition to other type of predator.

Many lizards escape from predators such as birds and mammals by fleeing into the nearest refuge (Greene, 1988; Cooper, 1997). However, in some systems this simple and safe strategy may face lizards with other type of predator, because some saurophagous snakes live hidden in rock crevices waiting for lizards. Thus, the gecko *Oedura lesueurii* shares the same refuges than one of its main snake predators (*Holocephalus bungaroides*). However, geckos used their chemosensory ability to avoid entering rock crevices covered with the snake scent (Downes & Shine, 1998). When a refuge is unsafe (e.g. because it contains predator chemical cues), the probability of being detected by a second predator hidden in that refuge increased with time spent in the refuge. Hence, a prey hidden in an unsafe refuge would have increased costs of refuge use and should emerge from the refuge sooner than a prey hidden in a predator- free refuge .

Wall lizards *(P. muralis),* responded to simulated predatory attacks of a human by hiding inside rock crevices, and when this simulated predation pressure increased, lizards increased time spent in refuges (Martín & López, 1999b). However, by increasing refuge use, wall lizards may expose themselves to increased predation risk by smooth snakes *(Coronella austriaca),* which inhabit rock crevices waiting for their lizard prey. Thus, wall lizards employed different alternative escape strategies in relation to their reliance in refuges (Amo, López & Martín, unpublished data). Lizards that were basking close to a refuge that had used before, used to hide in it again when suffered a simulated attack of the experimenter, whereas those that were moving not always enter the closest refuge, but often ran away without hiding. This alternative strategy that avoid to use refuges might be related to the risk of encountering a saurophagous snake inside an unknown refuge.

Conclusions

Ecological requirements, such as foraging or thermoregulation, and antipredatory behavior (i.e. hiding in refuges) can be conflicting demands in lizards. However, lizards may resolve this conflict by optimization of time spent in the refuge to reflect a balance between predation risk upon emergence and costs of remaining in refuge, and by adjusting escape distances. For example, the ability to estimate short-term fluctuations in food availability or thermal environment and to take current nutritional status into account appear enable lizards to cope with changes in predation risk without incurring excessive costs in terms of lost foraging opportunities or physiological impairments.

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