Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits

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Abstract: The use of protective cover by prey animals is commonly associated with high predation risk. Rabbits (*Oryctolagus cuniculus*) in southern Spain use vegetated patches in daylight but open prairie during the night, although predation rates are high during both periods. Hiding under vegetation may be adaptive for rabbits during the day because they suffer predation by visually oriented birds of prey, but may be dangerous during the night, when they are hunted by carnivorous mammals that need cover to stalk. Therefore, the heavily predated Spanish rabbits may leave dense cover in nighttime and exploit the rich prairie food.

Résumé : L'utilisation d'abris chez les animaux qui servent de proies est souvent associé à des risques de prédation élevés. Dans le sud de l'Espagne, les lapins (*Oryctolagus cuniculus*) cherchent leur nourriture sous la couverture végétale à la lumière du jour, mais fréquentent les prairies ouvertes à la nuit, bien que les taux de prédation soient élevés au cours des deux périodes. L'utilisation du couvert de végétation par les lapins durant le jour est sans doute une adaptation, car à ce moment ils sont exposés aux oiseaux de proie qui chassent à vue, mais cette stratégie peut être dangereuse à la nuit car les mammifères carnivores se servent de la végétation pour se mettre à l'affût. C'est pourquoi les lapins d'Espagne, victimes fréquentes des prédateurs, quittent la végétation dense à la nuit pour exploiter la nourriture riche des prairies.
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Introduction

An individual's risk of predation varies over time and from place to place, depending on such factors as the amount of cover, the type of predator, and visibility (Hughes and Ward 1993; Power et al. 1992; Lima 1988). In addition, foraging benefits also vary and frequently conflict with antipredator behaviour, so individuals are forced to trade the benefits of foraging against the need to reduce the risk of predation (Brown 1988). In consequence, to select their "enemy-free space" (Jeffries and Lawton 1984), prey animals must be able to assess their vulnerability under different circumstances of time, habitat, and predator type and incorporate this information into their decision making (Lima and Dill 1990).

The European rabbit (*Oryctolagus cuniculus*), native to Mediterranean Spain and introduced into many parts of the world (Thompson and King 1994), is prey for a large number of species in its area of origin but for fewer species where it has been introduced (Delibes and Hiraldo 1981; Jaksic and Soriguer 1981). Assuming that predation risk increases with distance to cover, as found in many animals from small fish (Werner et al. 1983) to passerines (Grubb and Greenwald 1982) and rodents (Hughes and Ward 1993), it has been proposed that rabbits will forage close to protective cover in Spain but in open habitats in the less dangerous areas where it has been introduced (Jaksic et al. 1979; Jaksic and Soriguer 1981). This hypothesis implies that in Mediterranean Spain rabbits would not use the abundant and high-quality foods available in the open areas (Lazo 1992).

In this study we investigate in more detail the ability of native European rabbits to vary their use of microhabitat on a circadian basis. We investigated the hypothesis that variation in predation risk and type of predator with time of day causes rabbits to alter their spatial behaviour.

Methods

Study area

The data were collected in Doñana National Park (approximately 37°10′N, 6°23′W), an area of approximately 550 km^2 at the mouth of the Guadalquivir River. The climate is Mediterranean subhumid, with hot dry summers and mild rainy winters. The park comprises three main biotopes (marshes, Mediterranean scrubland, and dunes; Valverde 1958), and rabbits are particularly abundant in the scrub and at the edge of the marsh, a grassland area (Rogers and Myers 1979).

Risk of predation

The relative risk of predation from each predator species was defined as the probability of being killed by this species, and was calculated from a parallel study by one of us (Villafuerte 1994), which recorded each loss due to predation from a radio-marked sample of the rabbit population in the same area. As this estimation of risk relies on the net losses of rabbits due to each predator species, consideration of the abundance of individual predators is

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irrelevant. Predation on baby rabbits still in the nest was not considered.

To estimate the relative risk of predation at night and during the day, and in open and vegetated patches, we assumed that (*i*) each predator species hunts rabbits during the period when it is usually active, and (*ii*) diurnal birds of prey, which detect prey by sight, usually take rabbits in open patches (Janes 1985), while terrestrial carnivorous mammals, which need cover to stalk or approach rabbits (Murray et al. 1995), take them in vegetated patches.

Habitat use

To compare the relative use by rabbits of open and shrub habitats, four transects of various lengths (800, 600, 750, and 900 m) were selected along the border between scrub and grassland. We drove along these transects at a constant speed of 10 km/h and estimated the perpendicular distance from each rabbit sighted to the edge of the scrub (categorised as $x < 2$ m, $2 > x < 6$, $6 > x < 18$, and $x > 18$ m). These transects were driven nine times during daylight (about noon) and four times during the night (midnight) using a spot light. The data were collected in June 1986 during a period of sunny weather and a waxing moon.

Results

Risk of predation

Of the predator species regularly sighted in Doñana National Park during the spring, at least 16 have been reported to prey upon rabbits. These include 6 mammal species (4 nocturnal, 1 crepuscular–nocturnal, and 1 diurnal) and 10 birds of prey (8 diurnal and 2 nocturnal). However, some of these species (e.g., the genet, *Genetta genetta*, Palomares and Delibes 1991; the kestrel, *Falco tinnunculus*, Fernández 1985; the barn owl, *Tyto alba*, Herrera 1974) rarely eat rabbits, while others are rabbit specialists but very scarce (e.g., the endangered Iberian lynx, *Lynx pardinus*, Delibes 1980*a*). Eight species are responsible for most rabbit predation (accounting for 100% of a sample of 28 kills of radio-tracked individuals; Villafuerte 1994), including four diurnal birds of prey (*Milvus milvus*, *Milvus migrans*, *Hieraetus pennatus*, and *Aquila adalberti*), one diurnal carnivore (*Herpestes ichneumon*), and three nocturnal carnivores (*Vulpes vulpes*, *Meles meles*, and *Lynx pardinus*; the last-mentioned species was considered nocturnal, although its pattern of activity is flexible, because it is rarely active in the middle of the day; Beltrán and Delibes 1994). While the four birds of prey detect prey mainly by sight and capture them in the open, all the carnivorous mammals are primarily stalkers, relying on hearing and smell to detect and capture their prey in the scrub, in the border between scrub and prairie, and inside warrens (mainly located in the scrub).

As shown in Table 1, birds of prey are responsible for approximately half the observed rabbit mortality due to predation, while the carnivorous mammals account for the rest. The overall risk of predation, as defined above, is higher during daylight hours. The risk of being hunted would be negligible for rabbits in open areas at night and low in closed areas during the day. In this situation, we predicted that rabbits would use open habitat at night and the scrub during the day.

Habitat use

The data collected along the transects confirmed our prediction. The spatial distribution of the rabbits with respect to the edge of the scrub differed strongly between the day and night transects, rabbits preferring to feed close to cover during the day and farther from cover at night. The results were consistent in the four areas (Fig. 1). During the day, 70% of the observed rabbits were within 2 m of cover, while only 0.5% were farther than 18 m. In contrast, at night, 7.9% of the rabbits were less than 2 m from cover, while 41.9% were at least 18 m from it. Moreover, rabbits are more active at night than during the daytime (number sighted daily (mean ± SD) = 63.25 ± 23.5, $n = 4$, and 21.9 ± 14.7, $n = 9$, respectively).

Table 1. Predation risk at two times of the day and in two microhabitats, estimated from the percentages of rabbits killed by birds of prey and carnivorous mammals (according to Villafuerte 1994).

	Midday		Midnight		
Microhabitat	Scrub	Open	Scrub	Open	Total
Birds of prey	0.0	53.3	0.0	0.0	53.3
Carnivorous mammals	11.6	0.0	35.1	0.0	46.7
Total	11.6	53.3	35.1	0.0	100.0

Note: We assumed that each predator species hunted rabbits during its usual activity period and in its usual microhabitat type.

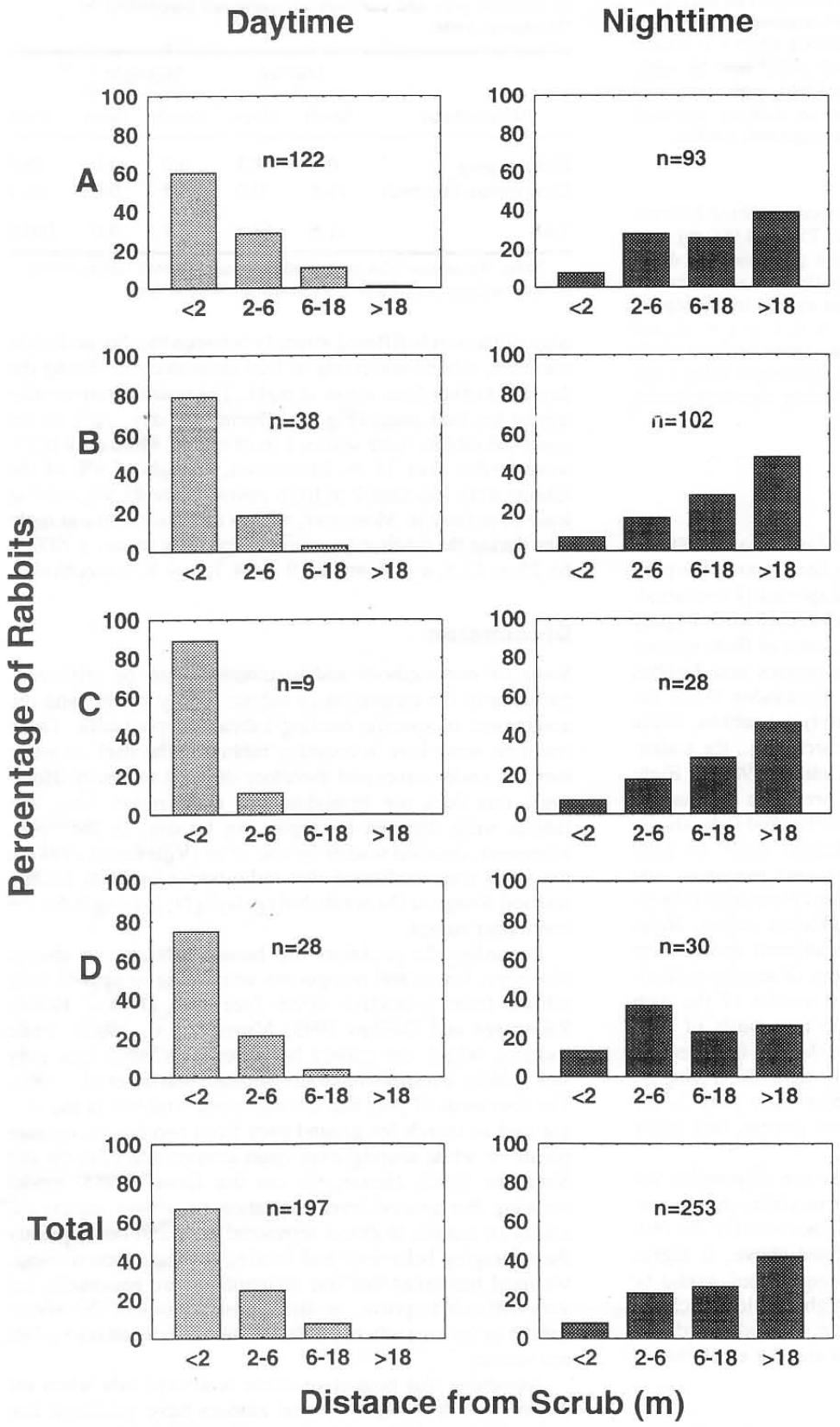
Discussion

Some of our methods and assumptions can be criticized, particularly the estimation of habitat use by rabbits and the assignment of specific hunting habitats to predators. There could be some bias in counting rabbits in the dark or when they are under cover and therefore difficult to detect. However, this does not invalidate our main result, i.e., that rabbits were detected by night, not by day, in the open. Moreover, detailed studies by one of us (Villafuerte 1994) in the same area confirmed that radio-tracked rabbits usually rest and forage in the scrub during daylight, leaving it for the open after sunset.

Regarding the predators that hunted habitats, we always saw lynx, foxes, and mongooses ambushing or approaching rabbits from protective cover (see also Delibes 1980*b*; Palomares and Delibes 1993; Murray et al. 1995), while badgers, which are mainly harvesters, probably take only sick rabbits irrespective of the habitat (Martín et al. 1995). The four birds of prey that usually capture rabbits in the area are said to search for ground prey from perches on vantage points or while soaring over open countryside (Cramp and Simmons 1980). Hence, we can use Janes' (1985) model showing that ground-level vegetation negatively affects the ability of raptors to detect terrestrial prey and consequently their foraging behaviour and hunting success. Nevertheless, we must recognize that our assumptions are reasonable but very difficult to prove, as direct observations of the microhabitat in the area where predators successfully attack rabbits are scarce.

Assuming that protective cover is always safe when the predation risk is high, several authors have predicted that under high predation risk (in southern Spain, for instance, where predators are abundant; Delibes and Hiraldo 1981), rabbits will forage under or close to cover, while under low

Fig. 1. Proportions of rabbits observed in the four intervals of distance to scrub in four different transects (A–D) and in total during daytime and nighttime.



predation risk (for instance, where they have been introduced and predators are fewer), they will prefer to forage in the more profitable open areas (Jaksic et al. 1979; Jaksic and Soriguer 1981).

Our results indicate that rabbits use open areas in Mediterranean Spain despite the high predation pressure. Although the percentage of rabbits actually killed by each predator does not provide exact information about the individual risk for rabbits using each habitat at each time, it strongly suggests that the risk of predation can be higher close to cover at some times of day.

The rabbits at Doñana show a clear preference for feeding in open areas at night and stay close to cover during the day (see also Villafuerte 1994). While it is to be expected that during the day rabbits would remain close to protective cover that provides protection from aerial predators, the selection of open areas at night, when they suffer 35.1 % of the total predation, seems contrary to the usual finding that animals feed close to cover where and when the risk of predation is high (Lima and Dill 1990). However, under certain circumstances dense vegetation may be a high-risk habitat, because mammalian predators use dense cover to stalk (Schaller 1972; Stander and Albon 1993) and their success depends on not being seen by their prey (Elliott et al. 1977). By using open areas at night, rabbits increase their chances of detecting approaching carnivorous mammals, their only predators at this time. Moreover, small carnivores such as genets, wildcats (*Felis silvestris*), badgers, and foxes may be less effective predators farther from cover, as they may themselves be vulnerable to predation by the larger Iberian lynx (Palomares et al. 1995).

Such use of vegetated areas during the day and open areas at night has also been described for other medium-sized prey animals (e.g., gray partridges, *Perdix perdix*; Birkan and Jacobs 1988) that suffer predation from diurnal birds of prey and nocturnal carnivores. Also, daily changes in microhabitat use to reduce the predation risk from different types of predator occur in other ecosystems. For example, diurnal wading predators such as herons can exclude small fish from shallow water during the day, while swimming predators can push them into shallow water at night (Schlosser 1988).

For rabbits, this daily shift in habitat use is also a response to the trade-off between maximizing energy gain and minimizing predation risk. Restricting their foraging activities to shrubs to avoid predators, as previously suggested by Jaksic and Soriguer (1981), would prevent the rabbits from exploiting the abundant food supplies on the open prairies. Studies in the same area and the same month but some years later showed that the availability of pasture (estimated as dry biomass per hectare) was four to six times greater on the open prairie than in scrubland (Lazo 1992).

Although it seems most likely that rabbits feed farther from cover at night to exploit grassland while avoiding terrestrial predators, there are alternative explanations for our results. For instance, rabbits could use open areas more frequently at night for thermoregulatory reasons (Villafuerte et al. 1993), or differential habitat use might be related to reproductive strategies, as was found for *Lepus americanus* (Litvaitis 1990). In any case, our results suggest that cover is not always a safe and preferred habitat for European rabbits in Mediterranean Spain, as was previously thought.

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