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# BEHAVIORAL THERMOREGULATION BY TREECREEPERS: TRADE-OFF BETWEEN SAVING ENERGY AND REDUCING CRYPSIS

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*Abstract.* We studied the effect of solar radiation on the winter biology of Short-toed Treecreepers *Certhia brachydactyla* inhabiting a montane forest in Spain. We hypothesized that, in temperate latitudes of cold winter climate, with low cloudiness and under windless conditions, birds should select sunlit sites (i.e., forest sectors or trunk patches with high levels of exposure to sunlight) to reduce the metabolic cost of thermoregulation. At a within-habitat scale, a hypothesis of ''only metabolic benefits'' predicts that birds should select sunlit patches at shade temperatures ($T_{\text{shade}}$) below the birds' lower critical temperature ($T_{\text{lc}}$). They should shift to a random use of sunlit and shaded patches at temperatures above $T_{\text{lc}}$. Alternatively, there could be added costs (e.g., travel costs, predation risk) in using sunlit patches. If higher visibility leads to diminished crypsis at sunlit patches (''trade-off with predation risk'' hypothesis), birds should select only shaded patches at $T_{\text{shade}}$ values above $T_{\text{lc}}$ (to enhance crypsis). They should increasingly select sunlit patches as $T_{\text{shade}}$ decreases below $T_{\text{lc}}$.

Treecreepers were selective in their use of sun–shade patches, across different spatial scales. At the among-plots scale, treecreeper abundance was positively related to the availability of sunlit trunks, after we controlled for the effects of tree density, prey availability, and altitude. At the within-plot scale (i.e., selection of foraging patches on trunks and thick branches), Ivlev's electivity for sunlit patches decreased linearly as $T_{\text{shade}}$ increased. Birds preferred to forage on sun-exposed surfaces (electivity $>0$) when $T_{\text{shade}}$ was lower than $\sim 4°\text{C}$, but they tended to forage on shaded surfaces (electivity $< 0$) when $T_{\text{shade}}$ was higher than $\sim 9°\text{C}$. The selection of sunlit trunk patches at low temperatures was not a by-product of higher food availability, because numbers of prey were much less predictable than temperature as a function of trunk exposure (sun vs. shade), and the negative relationship between use of sunlit patches and temperature remained significant when we controlled for the effects of prey availability. Thus, the selection of sunlit patches at low temperatures can be interpreted as a behavioral thermoregulation strategy allowing birds to save energy. However, the Ivlev's electivity for sunlit patches became negative at temperatures well below $T_{\text{lc}}$, and no sunlit patches were used when $T_{\text{shade}} \approx T_{\text{lc}}$, which led us to reject the ''only metabolic benefits'' hypothesis.

Photometric measurements of treecreeper taxidermic mounts realistically positioned on trunk surfaces, and detection times by simulated (human) predators, suggest that treecreepers were more detectable under direct solar radiation than in deep shade. Crypsis diminished in sunlit patches because of a higher image contrast and an increased difference in perceivable coloration between bird and background, relative to shaded patches. Average detection times were significantly lower for sunlit mounts. Moreover, focal birds scanned more frequently in sunlit than in shaded patches. Thus, the observed temperature-dependent variation in the selection of sunlit substrata is consistent with the ''trade-off with predation risk'' hypothesis predicting that prey should avoid patches where they are more detectable to potential predators. We interpret the distribution and behavior of treecreepers as indicative of a trade-off between the energy savings (through higher operative temperature and reduced metabolic costs) and the increased risk of predation (through higher visibility and diminished crypsis) afforded by sunlit foraging patches.

*Key words: avian energetics; behavioral thermoregulation; bird abundance;* Certhia brachydactyla; *crypsis; endotherms; food availability; predation risk; temperature; trade-off; treecreepers.*

## INTRODUCTION

The need to maintain a favorable energy balance is one of the potential factors influencing bird abundance and distribution. Small passerines have high relative energy requirements (Walsberg 1983, Blem 1990, Hedenström 1992) because of the small thermal inertia caused by their high surface/volume ratio and the high metabolic cost of flight (9–23 times the basal metabolic rate; Tatner and Bryant 1986, Carlsson and Moreno 1992). In winter, these requirements rise as a conse-

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quence of the inverse relationship between metabolic rate and ambient temperature (Calder and King 1974, Moreno et al. 1988). The long, cold winter nights impose additional energy costs, causing some small passerines to lose $>$10% of their body mass overnight (see Bednekoff et al. 1994 and references therein), and eventually threaten their winter survival.

Thermoregulation made up $\sim$42% of the total daily energy expenditure in aviary-housed Loggerhead Shrikes (*Lanius ludovicianus*) with probable low locomotory costs and in Chukars (*Alectoris chukar*) during winter time, with daily operative temperatures $\sim$5–25°C (Weathers et al. 1984 and Carmi-Winkler et al. 1987, respectively). Thus, any physiological or behavioral strategy that could reduce the metabolic cost of thermoregulation might help to enhance winter survival. One such strategy is to gain environmental heat from external sources, particularly radiation, which has a pronounced effect in reducing thermoregulatory costs at low temperatures (Hamilton and Heppner 1967, Lustick et al. 1970, Ohmart and Lasiewski 1971, De Jong 1976, Lustick et al. 1978, 1980). Thus, birds inhabiting cold environments should select the patches or localities with a higher incidence of solar radiation. This form of behavioral thermoregulation could be especially relevant in mid-latitude montane regions, where winter temperatures usually remain below 0°C, but there is a greater availability of calm, longer sunny days than in higher latitudes.

At a regional, coarse-grained scale, we therefore predict that the winter abundance of small passerine species should be positively related to the amount of solar radiation received by different localities or habitat sectors. However, such a relationship could be obscured by between-plot differences in food availability or habitat structure, which means that any study designed to examine its importance should control statistically for the effects of these confounding variables.

### *A model for the behavioral selection of sunlit vs. shaded patches*

At the within-habitat scale, other factors may influence the exploitation of sun–shade patches. To work out our predictions, we make the following assumptions. (1) It is well known (Calder and King 1974) that, in the absence of convective heat losses (e.g., windspeed $\approx$0 m/s), metabolic expenditure decreases with increasing temperature at temperatures below the lower critical temperature ($T_{\mathrm{lc}}$), and it remains constant within the thermoneutral range (Fig. 1A). (2) The environmental temperature experienced by birds is always higher in sunlit than in shaded patches ($\Delta T = T_{\mathrm{sun}} - T_{\mathrm{shade}} > 0$; $\Delta T \approx$ 10–15°C in our study area; Mozetich 1995). (3) The temperatures available in temperate cold areas are always below the upper critical temperature ($T_{\mathrm{uc}}$ in winter), which implies that there are no thermoregulatory costs to the use of sunlit patches (e.g., due to overheating or evaporative water loss; Austin 1976, Weathers and Greene 1998).

Given the shape of the metabolism–temperature relationship (Fig. 1A) and the positive value of $\Delta T$, the thermoregulation benefit of using sunlit patches should vary with temperature, as shown in Fig. 1B: constantly maximum when $T_{\mathrm{shade}} < T_{\mathrm{lc}} - \Delta T$, monotonically decreasing between $T_{\mathrm{lc}} - \Delta T$ and $T_{\mathrm{lc}}$, and no benefit when $T_{\mathrm{shade}} \geq T_{\mathrm{lc}}$. Under windless conditions, a theoretically optimal pattern of behavior (using metabolic savings as the only relevant currency for short-term decisions) would imply selecting only sunlit patches when $T_{\mathrm{shade}}$ is lower than $T_{\mathrm{lc}}$, because thermoregulation benefits on sunlit patches are always positive. When $T_{\mathrm{shade}}$ reaches the thermoneutral range, birds should shift to a random use of sun–shade patches. This shift could follow a step function (continuous line in Fig. 1C: ‘‘only metabolic benefits’’ hypothesis) if there were no added costs to the use of sunlit patches, an assumption that is unlikely on two major grounds (for zero–one rules, see Stephens and Krebs 1986). First, the availability of sun-exposed surfaces is expected to change with time of day. Early in the morning, for instance, there is a low availability of sunlit patches and environmental temperatures are low. Therefore, a continuous exploitation of sunlit patches is constrained by their scarcity and associated high travel costs between them.

Second, and perhaps more important, detectability to potential predators might increase at sunlit patches relative to shaded ones, and this could lead to an increased risk of predation. Maximum predation risk naturally occurs at the highest light intensities, and light intensity can be used as a cue for predator avoidance (e.g., Clarke 1983, Watanuki 1986, Endler 1987, Clark and Levy 1988, Kotler et al. 1988, 1994, Wolfe and Summerlin 1989, Lima and Dill 1990, M. Díaz 1992; but see Bouskila 1995). However, surprisingly few studies document the existence of a trade-off between thermal benefits and increased visibility to predators in sunlit locations. Here, we hypothesize that such a trade-off might substantially modify the relationship between temperature and selection of sunlit patches by small birds. To proceed with this argument, we need to assume that detectability increases, and crypsis decreases, with light intensity (i.e., exposure to sunlight), so that predation risk should be higher at sunlit patches. A second assumption is that predation risk is independent of temperature, because it is illumination, not temperature, that causes birds to be more vulnerable to predators.

Figure 1D depicts the variation in the relative benefit of exposure to sun at different temperatures. When $T_{\mathrm{shade}}$ is lower than $T_{\mathrm{lc}} - \Delta T$, thermal benefits increase monotonically with time spent in full sun. At temperatures in the shade between $T_{\mathrm{lc}} - \Delta T$ and $T_{\mathrm{lc}}$ (e.g., $T_1$ and $T_2$, with $T_{\mathrm{lc}} - \Delta T < T_1 < T_2 < T_{\mathrm{lc}}$), the increase in thermal benefit reaches a plateau at different values of sun exposure, depending on the distance between $T_{\mathrm{shade}} + \Delta T$

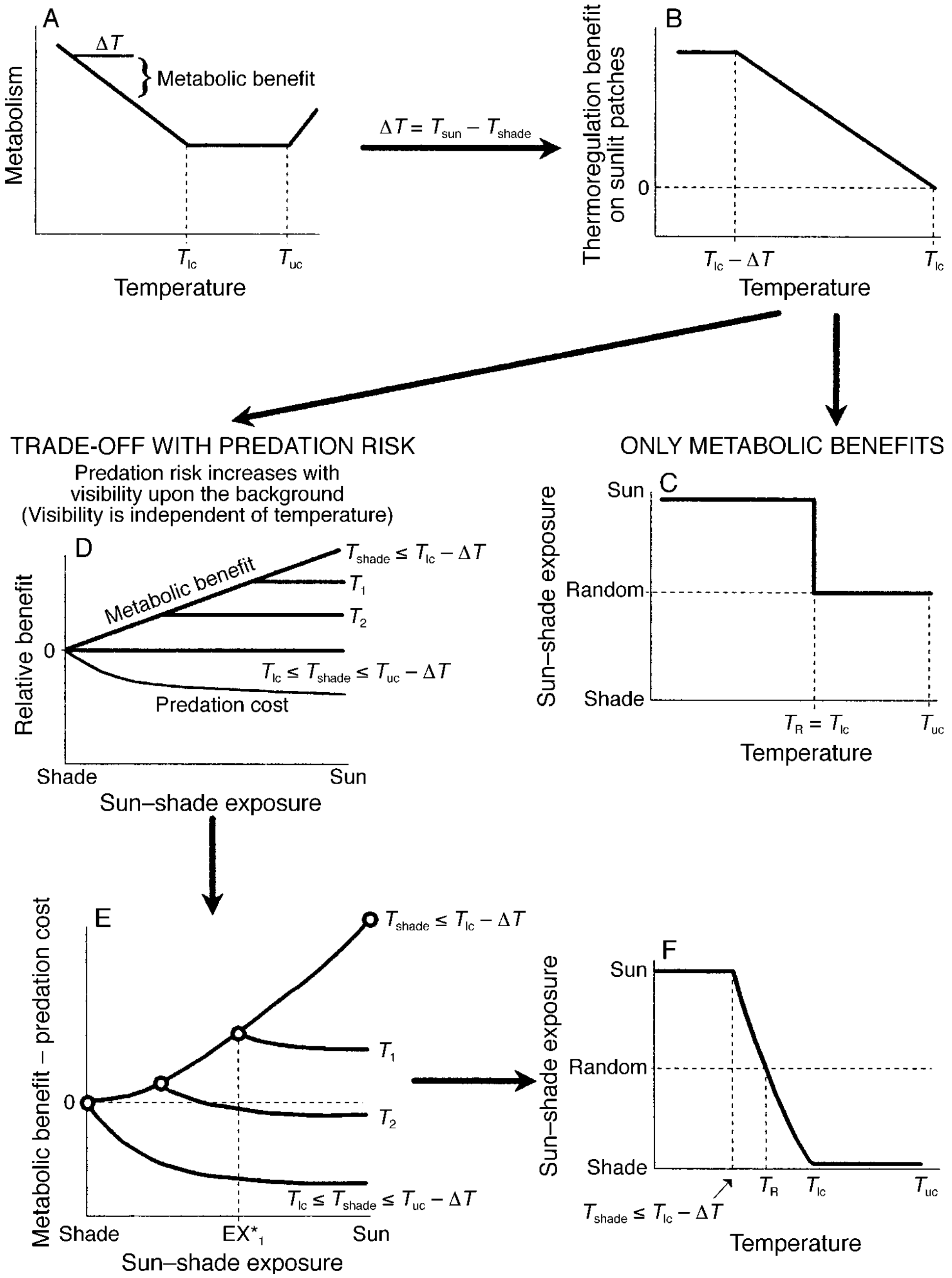

FIG. 1. A graphic model relating ambient temperature in the shade ($T_{shade}$), energy metabolism, and diminished predation risk due to enhanced crypsis at shaded patches with treecreeper exploitation of the environmental mosaic of sun–shade patches. This model applies only to ambient temperatures (both in sunlit patches [$T_{sun}$] and in the shade) lower than the upper critical temperature $T_{uc}$), such as those prevailing in temperate regions during the winter. Here, $EX^*_1$ is the maximum value for the "metabolic benefit minus predation cost" term attained for a given temperature $T_1$; $\Delta T$ is the temperature difference between sunlit and shaded patches; $T_{lc}$ is the lower critical temperature; and $T_R$ is the temperature at which the use of sunlit patches is unselective (i.e., proportional to its availability). Benefits refer to any common scale (e.g., energy or survivorship) on which energy saving and predation risk can be measured.

and $T_{lc}$. When we combine predation costs due to increased visibility at sunlit patches with metabolic benefits at different temperatures (Fig. 1E), we note that the optimal amount of exposure to sunlight becomes smaller as $T_{shade}$ approaches $T_{lc}$. For example, when $T_{shade}$ is lower than $T_{lc} - \Delta T$, the balance increases to reach a maximum at 100% exposure to sun, so that birds should only use sunlit patches. At temperature $T_1$, the balance increases up to a value $EX^*_1$ of exposure to sunlight (the maximum, or optimal sun–shade exposure that maximizes the trade-off between metabolic benefit and predation cost), and then decreases as exposure to sun keeps rising above $EX^*_1$. Finally, when $T_{shade}$ is in the range between $T_{lc}$ and $T_{uc} - \Delta T$, birds face only costs at sunlit patches (diminished crypsis with no thermal benefit), and they should remain in the shade. Representing the values of exposure to sunlight that maximize the balance between metabolic benefits and predation costs ($EX^*_i$ values for any $i$ temperature) against $T_{shade}$, we obtain Fig. 1F.

Thus, if all these assumptions are met, we predict three important changes in the shape of the relationship between selectivity for sunlit patches and temperature. First, selectivity for sunlit patches should decrease within the range $T_{lc} - \Delta T \leq T_{shade} \leq T_{lc}$, because the thermal benefits of sun exposure decrease as temperature approaches $T_{lc}$, whereas the risk of predation increases with exposure to sun. Second, birds within the thermoneutral zone should stay in the shade in order to enhance crypsis (because $T_{shade} \geq T_{lc}$ and sunlit patches provide no thermal advantage). Finally, the temperature at which birds randomly use sunlit and shaded patches ($T_R$ in Fig. 1F) will be lower than $T_{lc}$. Depending on how rapidly the risk of predation increases with sun exposure, this displacement toward lower temperatures will be more or less pronounced. Compare the predictions derived from the ‘‘trade-off with predation risk’’ hypothesis (Fig. 1F) with those derived from the step function model accounting only for metabolic benefits (i.e., zero–one rule, Fig. 1C).

It should be noted that our predictions will necessarily be qualitative because of a lack of information about thermal benefits and predation costs on a common scale. Moreover, an animal's $T_{lc}$ may vary seasonally, with time of day, and depending on whether the animal is in darkness or light, and fasted or replete. However, our graphic model (Fig. 1) is able to evaluate the ‘‘only metabolic benefit’’ hypothesis, independently of the exact values of parameters $T_{lc}$, $T_{uc}$ and the slope of the relationship of metabolism vs. temperature. Imprecision in the assessment of those parameters affects the slope and set point values of the curve in Fig. 1F, but not its markedly different graphic pattern as compared with Fig. 1C.

### *Objectives*

To test these predictions, we analyzed a natural, ecologically relevant scenario, considering a well-established physiological basis. Our model organism (a small insectivorous passerine) and our ecological system—(a cold montane forest in south western Europe) are appropriate for the questions being addressed. The bird of choice is the Short-toed Treecreeper (*Certhia brachydactyla*), an active insectivorous searcher that forages almost exclusively on tree trunks. On these feeding substrates, the availability of sunlit and shaded patches varies naturally within and between trunks, without being confounded with differences in vegetation structure (e.g., shelter) that might also condition the behavior of birds. This allowed us to identify a ‘‘pure’’ effect of illumination on crypsis by eliminating the confusion between visibility and structural safety. In other situations, the shaded site differed from the sunlit one not only in visibility, but also in the security afforded by the structures that provide shade and refuge (e.g., rock crevices, dense cover below shrubs, etc.; see Pianka 1986, Carrascal et al. 1992, J. A. Díaz 1992, Martín and López 1999).

Our specific goals were:

1) To analyze whether the spatial variation in treecreeper abundance is related to the amount of solar radiation received by different woodland plots, controlling for the effects of food availability and habitat structure.

2) To analyze whether the selection of sunlit trunk patches covaries with environmental temperature according to the predictions of a model considering only the metabolic benefits derived from exposure to sunlight.

3) To test whether treecreepers are more detectable or perceive higher risk in sunlit than in shaded patches, which would imply a trade-off between the thermal benefits of sun exposure and the predation costs derived from diminished crypsis at sunlit patches. An additional objective was to analyze whether a model considering such a trade-off can successfully predict the observed pattern of covariation between temperature and selection of sunlit patches.

## METHODS

### *Study area*

Data were collected in the Guadarrama range (central Spain, approximately 40°47′ N, 04°00′ W). This is a montane area mainly covered with coniferous forests of scots pine *Pinus sylvestris* from 1000 to 2000 m a.s.l. The axis of the range is west–east oriented, but there are many valleys with a north–south orientation. This land pattern defines a considerable amount of variation in the cardinal orientations of slopes and the amount of solar radiation received by different forest tracts.

Average duration of day : night time in this area during our study period (December–February) is 9.9: 14.1 h (daytime range: 9.25–10.5 h, nighttime range: 14.75–13.5 h). During the winter season, the area has a cold-continental mediterranean climate. Mean average temperature in December–February of 1997–1998 was 1.1°C at 1850 m a.s.l. (Navacerrada Pass), and mean minimum temperature during this period was −1.4°C. Although harsh winter snowstorms influence the climate of the area, anticyclonic conditions predominate during the winter season. Thus, 42% of the days in December–February of 1997–1998 were cloudless, with snow precipitation affecting 39% of the days. February is usually the sunniest winter month, with up to

74% cloudless days in 1997–1998. These data are representative of the long-term meteorological conditions prevailing at the study area, as indicated by the mean of 46% cloudless daytime hours computed for the whole Guadarrama range (1994–1995, CLIMATE database version 2.1, W. Cramer, Potsdam, Germany, *personal communication*).

Short-toed Treecreepers were censused in pine forests throughout the area within the 1500–2000 m a.s.l. altitudinal range. Below 1500 m, the Guadarrama range reaches the valleys of the Northern Spanish plateau, providing little variation in the orientation of slopes, and hence no differences in insolation. The behavior of treecreepers exploiting sunlit and shaded trunk surfaces was sampled in a large area of Valsain-La Granja mixed (pine–oak) forest at 1150–1500 m a.s.l. This area is covered by an ancient forest with very large trees, many higher than 20 m. Tree density is relatively low (100–200 trees/ha), thus facilitating the monitoring of long sequences of treecreeper's foraging behavior. Finally, photographs of stuffed treecreepers on sunlit and shaded trunks were taken in Los Asientos (Valsain-La Granja area).

### *Study species*

The Short-toed Treecreeper *Certhia brachydactyla* is a small (~8.2 g), insectivorous bird common in temperate forests of the southwestern Palaearctic. It occurs at middle and lower middle altitudes of temperate zones, becoming more montane at the southern edge of its range (Hagemeijer and Blair 1997). It is a strictly arboreal passerine that forages for arthropods on the trunks of practically any species of tree (Cramp and Perrins 1993). Winter populations show little evidence of movement other than postbreeding dispersal. In the Guadarrama montane woodlands, winter foraging is restricted to the trunks and thick branches of trees (mainly Scots pine, *Pinus sylvestris,* and Pyrenean oak, *Quercus pyrenaica*; Carrascal et al. 1987). The strictly insectivorous diet and the small size of this bird species make it an adequate model for the objectives of this study.

The lower critical temperature for the Short-toed Treecreeper is 21.5°C (data from winter-acclimated, postfeeding birds during nighttime; Mozetich 1995), a value that falls within the range 20–25°C obtained from allometric equations and from empirical data of phylogenetically related, similarly sized species (Calder and King 1974, Kendeigh et al. 1977).

### *Arthropod and ambient temperature variation with exposure to sun*

As an approximation to the environmental temperature experienced by foraging birds, we used hollow copper cylinders (length 5 cm, diameter 1 cm) closed at both ends except for a small fissure that allowed us to insert the sensing tip of an electronic digital thermometer (digi-thermo; ±0.1°C precision). We assume that these devices are not proper operative temperature thermometers (due to differences in coloration, insulation, and boundary-layer effects; Bakken et al. 1985, Bakken 1989). However, previous measurements showed that, on calm days, copper cylinders and taxidermic mounts (copper models covered by treecreeper skins) eventually reached the same equilibrium temperatures (see also Vitt and Sartorius 1999). Thus, copper models provided reasonably close approximations to the taxidermic mounts under the same conditions of radiant heat loads. At equilibrium, the temperatures of copper cylinders and taxidermic mounts were almost perfectly correlated ($R^2 = 0.9995$, $n = 15$, range 3–40°C; $T_{\mathrm{mount}} = 0.49 + 0.99\ T_{\mathrm{cylinder}}$). Therefore, our model temperatures reflect and quantify the thermal difference between sunlit and shaded locations under windless, cold, winter conditions. Nevertheless, we acknowledge that our measurements could be refined for wind plus temperature effects by incorporating a standard temperature scale that would predict selection of sites for increasing solar exposure and wind avoidance.

Prey availability for treecreepers was estimated by counting all arthropods >1 mm long found during 2 min at a height of ~1.5 m on the selected trunk (see Cooper and Whitmore 1990 and references therein). Arachnids and Diptera accounted for >80% of arthropod numbers both in sunlit and shaded locations. The scarcity of prey in shaded locations precluded any reliable statistical comparison of prey size or type between sunlit and shaded patches. However, it is unlikely that these variables differ markedly between sun and shade, because exposure to sun at a given trunk surface changes several times within a single day as a consequence of the shadows cast by other trees.

To assess the predictability of model temperature and food availability as a function of exposure to sun (sunlit or shaded trunk surfaces) and variation among individual trees, we recorded the temperature of the copper tubes and the availability of potential prey on 25 randomly selected trees in the Valsain area (1350 m a.s.l.) in February 1998. Estimates were repeated twice on the sunlit half of the trunk and twice on its shaded half, thus providing an overall sample size of 100 values for temperature and arthropods.

Significance of the effects was tested using a mixed repeated-measures ANCOVA model, with sun–shade as the fixed within-subjects factor, individual tree as the random factor, and time of day as the covariate. Variation between the two samples from each tree and sun–shade level defined the residual variance of the ANCOVA model. The partition of variance was estimated by means of a multiple regression approach to ANCOVA, with time of day, exposure to sun–shade, and individual tree (these later two factors coded as dummy variables) as independent variables.

### *Censuses*

The abundance of treecreepers was estimated by one of us (D. L. Huertas), at 20 different 5-ha transects, by counting all birds detected along two 25-m survey belts, one on each side of the progression line. Census transects were 1 km long (5 ha). Nearly all treecreepers were first detected by their calls. Treecreepers are not very noisy birds, but they continuously emit a clear call and are easy to locate (about one call every 2–5 min). Censuses were carried out between 0800 and 1200 (GMT, Greenwich mean time), always on calm, clear days. Each plot was censused twice (first in January and then in February 1998) and we used the mean of the two values as an estimate of treecreeper abundance. The incidence of solar radiation on each census plot was quantified by counting the number of trunks with at least half of their ''exploitable'' surface exposed to the sun along a 10 m wide belt at each side of the progression line. The exploitable surface of Scots pines extends over the entire circumference surrounding the lower part of trunks (~4 m), which has bark that does not flake away. The upper, flaked parts of trunks are avoided by foraging treecreepers (Carrascal 1988). The number of sunlit trunks was highly correlated with the duration of the daily insolation period (in hours per day) in each census plot ($r = 0.915$, $n = 20$, $P < 0.001$). Thus, plots receiving direct sunlight for a longer daily period, also had more sunlit trunks at midday. In addition, we also noted the altitude of each census plot and we controlled two other variables that might also condition treecreeper abundance (Carrascal 1987): the number of trees >30 cm in diameter at breast height, counted within a 25 m radius circle every 100 m along the transects, and the availability of potential prey, estimated by counting arthropods on the nearest trunk at every 100 m along the transects.

### *Selection of sunlit and shaded trunk surfaces by foraging treecreepers*

Focal samples of individual treecreepers were obtained by two of us (L. M. Carrascal and I. Mozetich) on clear, calm days in three different years (February of 1996, 1997, and 1998). Although focal birds were not marked for individual identification, the fact that samples were obtained in three different years, and throughout a large extension of pinewood (~100 ha), reduced the probability of repeatedly sampling the same treecreepers and thus precluded pseudoreplication. We tried to follow all individual treecreepers while we walked throughout the forest. Birds initially were detected mainly by ear. We followed focal birds from a distance of ≥15 m, without disturbing them, while they were foraging on pine trunks. Sampling times ranged from 1 to 10 min (145 ± 120 s, $\bar{X} \pm 1$ SD; $n = 36$ birds).

For each focal bird, we used a stopwatch to record the time spent in full sun and in shaded portions of trunks. At the end of each sample (truncated at 10 min, or when it became impossible to keep following the focal bird), we measured model temperatures and counted all arthropods found at breast height during 2 min, in all pine trees used by treecreepers, both in full sun and in the shade.

Availability of exploitable trunk surfaces exposed to the sun was visually estimated (at 20% intervals) in the 10 nearest trunks around the pines exploited by treecreepers. For those focal birds that foraged in more than one pine, we averaged estimates of sun availability over all of the exploited trunks.

In summary, for each focal bird, we estimated the percentage of time foraging in full sun, the average availability of arthropod prey on sunlit and shaded bark surfaces, the model temperature in full sun and in the shade, and an approximation of the average availability of trunk surfaces exposed to the sun.

Selection for sun patches was calculated by means of Ivlev's electivity index (Ivlev, 1961):

$$\mathrm{IE} = (P_\mathrm{f} - P_\mathrm{a})/(P_\mathrm{f} + P_\mathrm{a})$$

where $P_\mathrm{f}$ is the proportion of time spent foraging in the sun and $P_\mathrm{a}$ is the proportion of the exploitable trunk surface that is exposed to full sun.

### *Treecreeper detectability on sunlit and shaded trunk surfaces*

We used 20 slides of a stuffed treecreeper simulating a foraging posture on a tree trunk to examine whether the detectability of treecreepers differed between sunlit and shaded patches (Fig. 2; sample size was 10 in both illumination conditions). Stuffed birds were obtained from the bird collection at the Museo Nacional de Ciencias Naturales (Madrid, Spain). We asked a group of skilled birdwatchers (staff of the Vertebrate section at the Universidad Complutense of Madrid) to find the bird in the projected slides, and measured their detection times. Our aim was to detect differences between sun and shade in detectability for humans and perhaps other diurnal, visually guided predators, e.g., Sparrowhawks *Accipiter nisus*, weasels *Mustela nivalis*, and feral and wild cats *Felis* spp. We also applied a photogrammetric approach to test the hypothesis that such differences could be based on differences between sun and shade in (1) image contrast and (2) color disparity between bird and background.

Pictures were taken with a 35-mm tripod-mounted camera (Nikon F90N) with a 70–210 mm telezoom. The film used was Fujichrome Sensia II 100 ASA. All pictures were taken with a 81A filter. The diaphragm was f11 in all pictures to maximize depth of field and sharpness (especially in slide corners). We used the circular markings of the spot-metering area on the viewfinder as visual guides to establish the relative size of treecreepers and to achieve a similar size in all pictures. The tripod was located at a distance of 4.5–7 m from the trunk where the stuffed treecreeper was placed (at 1.0–1.7 m above the ground), and the focal length of the lens was zoomed between 135 and 180 mm. The picture area was divided into 12 sectors (three vertical by four horizontal sectors), and we randomly asigned

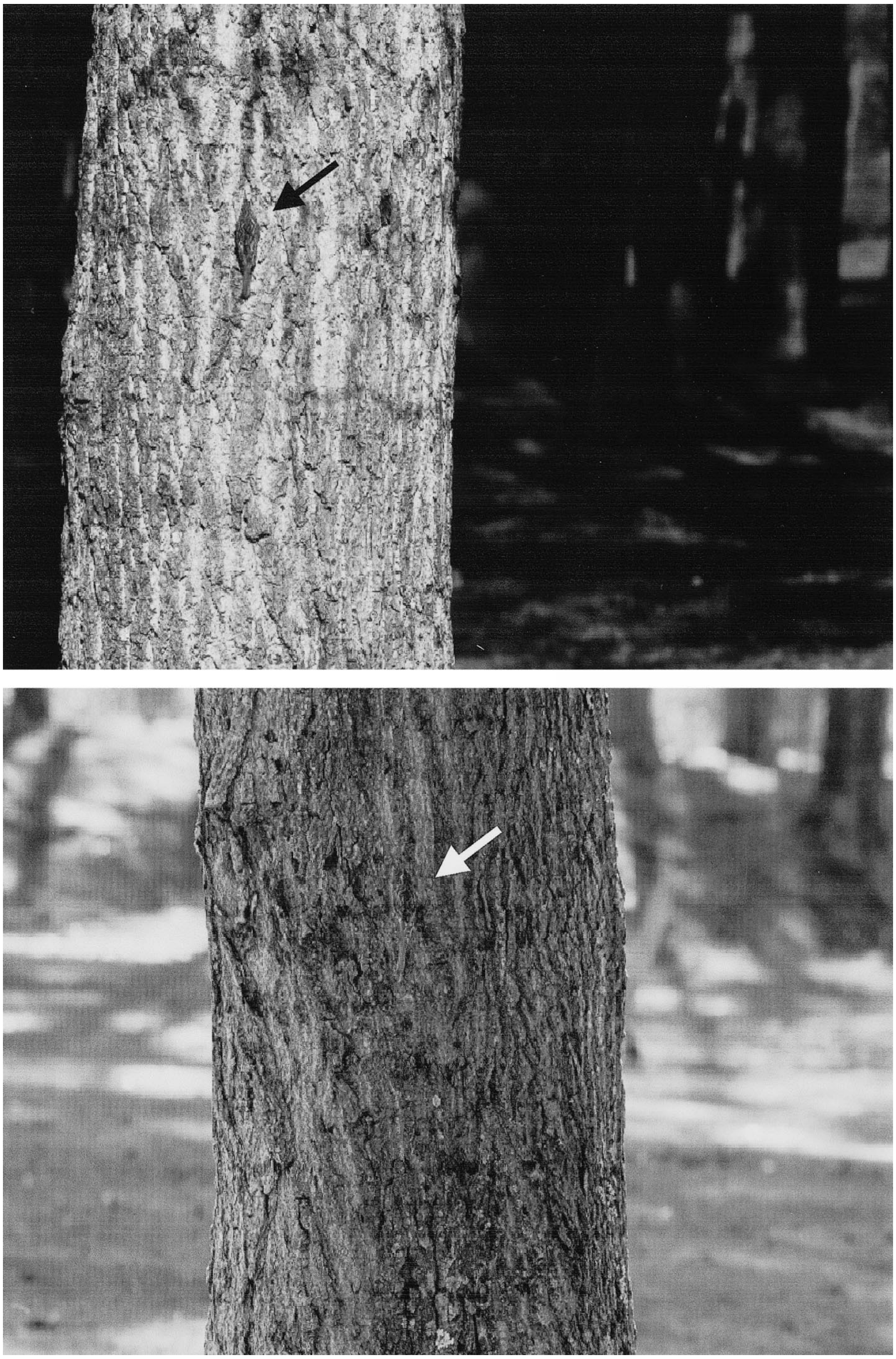

FIG. 2. An example of the stuffed bird slides used to obtain photogrammetric measurements and detection times of simulated (human) predators, both at sunlit (upper) and shaded (lower) locations.

treecreeper position to one of these sectors. Therefore, there were no spatial cues to locate treecreepers on slides when pictures were presented to observers.

Slides were digitized using a Polaroid Sprint Scan 35 plus film scanner (1774 × 1124 pixels; file size 5.7 Mb; Polaroid Corporation, Cambridge, Massachusetts, USA). We defined an area approximately three times the surface of the taxidermic mount (number of pixels = 20,541 ± 455, mean ± 1 SE; ~75 × 275 pixels) to carry out photogrammetric measurements of image contrast. We used Adobe Photoshop v4.0 (Adobe, San Jose, California, USA) to calculate, for each slide, the interquartile range of the distribution of pixels on a gray-scale single-channel image consisting of up to 256 levels of gray. This range provides a direct index of image contrast. The dark shadow produced by a bird in full sun, for example, originates a bimodal distribution of pixels, with a first peak at the lowest part of the scale (the shaded portion of the image) and a second peak at its brighter half (the sunlit portion).

We also measured color differences between bird (mount) and background (trunk surface excluding the mount). Color disparity was estimated as the absolute value of the difference between the bird and trunk mean levels of the distribution of pixels in the red, green, and blue channels (RGB scale) provided by Adobe Photoshop v4.0. We tested for the effect of exposure to sun or shade on color difference using a MANOVA model with red, green, and blue as the dependent variables.

Human detection times were tested by passing the slides to a group of 14 birdwatchers who were asked to find (and to confirm with a laser pointer) the location of the bird from a distance of 4 m. Slides were classified according to the situation of the taxidermic mount (in the sun or in the shade). Birdwatchers were questioned one by one. The size of the projected image on the screen was 1.5 × 1 m, the actual length of the stuffed treecreeper being ~17 cm. When birds were detected, detection times were measured with a stopwatch to the nearest 0.5 s, up to a maximum searching time of 1 min.

### *Vigilance and foraging on sunlit and shaded trunk surfaces*

In January–February 1998, we (L. M. Carrascal and J. A. Diaz) observed the behavior of focal birds as they foraged in the sun ($n = 24$ sequences) or in full shade ($n = 28$ sequences) in a large tract of a mature forest where treecreepers were very abundant. We tried to avoid repeated sampling of the same individuals by searching in different forest zones. The duration of behavioral sequences was 53.2 ± 29.4 s (mean ± 1 SD; range 15–126 s). For each focal bird, we noted sun exposure and time of day, counted the number of pecks, and measured with a stopwatch the total amount of time spent vigilant and the overall duration of the sequence. Scanning behavior was defined as the time that a bird spent motionless with its beak raised to eye level or higher (for a similar approach, see Hogstad 1988).

## RESULTS

### *Predictability of temperature and arthropod availability as a function of exposure to sunlight*

Exposure to sun ($F_{1,24} = 2289.4$), individual tree ($F_{24,24} = 9.4$), the interaction between both factors ($F_{24,25} = 7.2$), and time of day (multivariate effect of covariate: Rao's $R = 7.7$, df = 2, 23) had a significant effect on the temperatures available (all $P$'s $< 0.005$). Thus, temperature was consistently higher in the sun ($\bar{x} = 26.7$°C in the sun vs. $\bar{x} = 12.1$°C in the shade), and some particular trunks had higher temperatures than others. In addition, the magnitude of the temperature difference between sun and shade varied among individual trees. These latter effects are probably related to the previous thermal history of each trunk (e.g., trunks that were in the shade when temperature was registered, but were exposed to sunlight a short time before). The combined effects of exposure to sun, individual tree, and time of day explained 92.3% of the variance in operative temperatures, of which as much as 82.2% corresponded to differences between sun and shade.

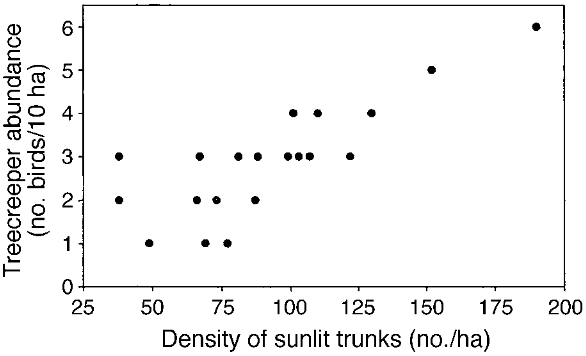

FIG. 3. Regression of treecreeper abundance against the number of sunlit trunks per transect.

Two factors, exposure to sun and individual tree, had a significant effect on arthropod counts (exposure to sun: $F_{1,24} = 33.8$, $P < 0.001$; tree: $F_{24,24} = 2.24$, $P = 0.027$), with larger numbers of prey on sunlit trunk surfaces ($\bar{x} = 2.9$ arthropods/2 min of search vs. $\bar{x} = 0.5$ in the shade). Neither the interaction between both factors ($F_{24,25} = 1.7$, $P = 0.107$) nor the effect of time of day (multivariate effect of covariate: Rao's $R = 2.7$, df = 2, 23, $P = 0.126$) was significant. The combined effects of exposure to sun, individual tree, and time of day explained 51.4% of the variance in arthropod counts, of which only 18.4% corresponded to differences between sun and shade, whereas 32.9% was accounted for by differences among trees. Therefore, food availability was less predictable than temperature, on the basis of the simple cue provided by the sun–shade dichotomy.

On a regional scale (i.e., differences among the 20 census plots), radiation and elevation together explained 33% of the among-plots variance in mean numbers of arthropods ($F_{2,17} = 4.2$, $P = 0.033$), of which 13.6% corresponded to the effect of radiation (partial standardized regression coefficient, $\beta = 0.380$, $P = 0.072$) and 19.4% to the effect of elevation ($\beta = -0.452$, $P = 0.036$). Thus, the altitudinal location of census plots was a better predictor of food availability than the incidence of solar radiation.

### *Covariation of treecreeper abundance and radiation levels*

The abundance of treecreepers was positively related to the availability of sunlit trunks (Fig. 3) when we

TABLE 1. Effect of independent variables on treecreeper abundance.

| Independent variable | β | $t$ | $P$ | % var |
|---|---|---|---|---|
| Log(no. arthropods) | 0.16 | 1.07 | 0.303 | 4 |
| No. sunlit trunks | 0.73 | 5.27 | <0.001 | 59 |
| Altitude | 0.38 | 2.56 | 0.022 | 13 |
| No. trunks >30 cm in diameter | −0.06 | 0.46 | 0.650 | 0 |

*Note:* Regression analysis: β = partial standardized regression coefficient; % var = percentage of variance explained, calculated as 100 × β × Pearson correlation coefficient; df = 15.

controlled for the effects of tree density, prey availability, and altitude (Table 1). Treecreeper abundance was also higher at higher altitudes, but it was unrelated to tree density or prey availability (Table 1). These four variables explained 76.2% of the variance in treecreeper abundance ($F_{4,15} = 12.0$, $P < 0.001$), the availability of sunlit trunks being its most useful predictor (59% of the variance explained).

### *Selection of sunlit and shaded trunk surfaces by foraging treecreepers*

The use of sunlit patches by focal treecreepers was negatively correlated with model temperature (weighted by the availability of sunlit and shaded trunk patches; partial standardized regression coefficient, $\beta = -0.787$, $P < 0.0001$) when we controlled for the effects of sun availability ($\beta = 0.111$, $P = 0.459$) and prey abundance, both in the sun ($\beta = 0.126$, $P = 0.437$) and in the shade ($\beta = 0.038$, $P = 0.811$). These four variables explained 51% of the variance in sun exposure among focal birds ($F_{4,31} = 8.07$, $P < 0.001$).

The selection for sunlit trunk patches exerted by foraging birds (Ivlev's electivity index) was negatively correlated with ambient temperature, independent of the particular temperature statistic employed, i.e., model temperature in the shade ($r = -0.778$; Fig. 4), in the sun ($r = -0.742$), or average weighted model temperature ($r = -0.787$, $n = 36$ and $P < 0.001$ in all cases). The regression line of electivity vs. $T_{\text{shade}}$ intercepts the 0 value of electivity at 6.5°C (95% confidence interval: 3.9–9.0°C). Thus, foraging treecreepers actively selected sun-exposed patches at low ambient temperatures (below ~4°C in the shade), but they preferred shaded locations when $T_{\text{shade}}$ was higher than ~9°C.

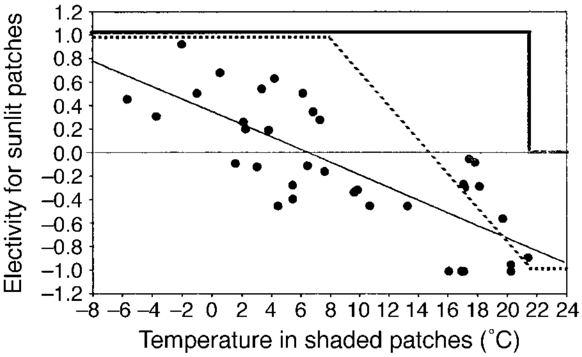

FIG. 4. Relationship between treecreepers' electivity for sun-exposed bark surfaces and the operative temperature in shaded patches. The thick, continuous line shows the predictions derived from the ''only metabolic benefits'' hypothesis (zero–one rule). The discontinuous lines show the predictions of the ''trade-off with predation risk'' hypothesis. For the temperature range between 8.0° and 21.5°C, the dashed line is only approximate, i.e., we predict a negative relationship between electivity and temperature, but the exact shape of such a relationship depends on the intensity of the predation pressure.

Fig. 4 also shows the comparison of our results with those predicted by the hypotheses of ''only metabolic benefits'' (zero–one rule; Fig. 1C) and ''trade-off with predation risk'' (Fig. 1F), based on the clear-cut graphic differences between both patterns. The data clearly lead us to reject the predictions of the ''only metabolic benefits'' model, because electivity for sunlit patches was negative (i.e., birds avoided sunlit patches) at $T_{\text{shade}}$ values well below the thermoneutral zone. Moreover, treecreepers did not continuously exploit sunlit patches when $T_{\text{shade}}$ was lower than $T_{\text{lc}}$ (~21.5°C), and a consistent pattern of shade seeking was observed above 7–8°C. On the other hand, our results partially mirror the predictions of the ''trade-off with predation risk'' model, because we found a negative relationship between electivity for sunlit patches and $T_{\text{shade}}$ at temperatures below $T_{\text{lc}}$. Nevertheless, data were inconsistent with predictions in that we did not observe a full selection of sunlit patches at temperatures lower than $T_{\text{lc}}$ minus $\Delta T$ (see *Introduction*). Selection for sunlit patches increased as temperature decreased, but no focal bird used only sunlit patches for foraging.

### *Treecreeper detectability on sunlit and shaded trunk surfaces*

The location of the stuffed bird in sunlit vs. shaded patches (Fig. 2) had a significant effect on the image contrast of its surrounding area (one-way ANOVA with image contrast log-transformed: $F_{1,18} = 57.85$, $P < 0.001$), the contrast being higher in the sun (interquartile range on a gray-scale single-channel image consisting of up to 256 levels of gray: $\bar{x} \pm 1$ SD = 59.4 ± 12.2, $n = 10$ slides) than in the shade (28.7 ± 6.0, $n = 10$ slides). Color disparity between the bird mount and its background (Fig. 5) was more pronounced in full sun than in the shade for the three color channels (Rao's $R = 4.42$, $P = 0.019$, df = 3, 16; Wilks' $\lambda = 0.55$). Thus, crypsis diminished in the sun not only

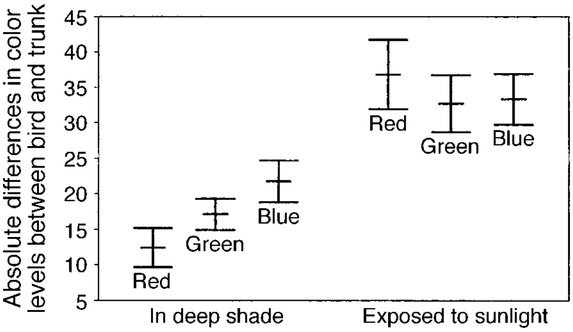

FIG. 5. Effects of the location of bird mounts (in full sun or in the shade) on the color discrepancy between bird and bark background. The *y*-axis shows the absolute value of differences in color levels in the RGB (red, green, blue) scale. Bars show means ± 1 SE ($n = 10$ in all cases).

because of the higher image contrast, but also because of an increased difference in perceivable coloration between bird and background.

All mounts in the sun were located by all observers in less than 1 min, and only three birdwatchers failed to locate the stuffed bird in less than 1 min when it was in the shade. Average detection times were significantly lower in the sun (1.2 ± 1.08 s, $\bar{x} \pm 1$ SD; $n = 10$ slides; the figure for each slide is the mean detection time for 14 observers) than in the shade (7.0 ± 3.8 s, $n = 10$; one-way ANOVA with detection times log-transformed: $F_{1,18} = 24.59$, $P < 0.001$).

### *Vigilance and foraging on sunlit and shaded trunk surfaces*

The proportion of time spent vigilant by foraging treecreepers (Table 2) was significantly higher in full sun than in the shade. Nevertheless, pecking rates did not differ significantly between sun and shade locations. The same analysis using net pecking rates (calculated discounting the time spent vigilant; i.e., roughly equivalent to net intake rates), yielded a similar nonsignificant difference. Therefore, food intake rates did not change with exposure to sun or shade, but treecreepers seemed to perceive a higher predation risk when foraging at sun-exposed locations.

## DISCUSSION

Our results show that Short-toed Treecreepers were selective in their use of sun–shade patches. This result was consistent at two different spatial scales. At the between-plots level, treecreeper abundance was positively related to the availability of sunlit trunks (determined by geomorphology and cardinal orientation of slopes). At the within-plot level, treecreepers preferred to forage on sunlit bark surfaces of trunks and thick branches when ambient temperature was low ($T_{\text{shade}}$ lower than ~6.5°C), and the intensity of the selection for sunlit patches was higher at lower temperatures. These patterns remained unchanged when we controlled holding for the effects of prey availability.

Although several authors have shown an association between temperature and the winter distribution of birds (northern limits and range size; Root 1988, Repasky 1991), little is known about the role that solar radiation might play in explaining and quantifying their distribution and abundance. This study, by documenting the influence of the radiative environment on the variation in treecreeper densities under conditions of cold stress, demonstrates the population effects of the thermal quality of the habitat (Huey 1991).

Solar radiation could exert its influence on the winter biology of treecreepers in three different ways. First, the radiation-induced increase in temperature could favor a reduction of thermoregulatory costs, because below the thermoneutral zone, metabolism falls as temperature rises (Calder and King 1974; see Fig. 1B). Second, temperature could have a positive, indirect effect on foraging efficiency through the activation of arthropods at higher temperatures (Avery and Krebs 1984, see also *Results*), which would lead birds in sunlit patches to achieve higher foraging success. Finally, the use of sunlit patches could also entail a higher predation risk via enhanced detectability on sun-exposed substrates (Endler 1987).

The concomitant effects of solar radiation on thermoregulation and foraging success were not controlled experimentally in this study, because all data were collected under natural conditions. However, our analytical approach allows us to statistically account for, and to estimate the magnitude of, each effect. Our conclusion is that arthropod availability did not significantly affect treecreeper distribution and behavior, and that the magnitude of its effect was negligible. Three sources of evidence support this conclusion. First, between-plot differences in food availability had a very low and nonsignificant influence on treecreeper density (accounting for 4% of variance). Second, exposure to sun or shade accounted for a low amount of variance (18%)

TABLE 2. Proportion of time spent vigilant and pecking rates of treecreepers while foraging in the shade ($n = 28$ observations) and in full sun ($n = 24$).

| Variable | Shade | Sun | $F_{1,50}$ | $P$ |
|---|---|---|---|---|
| Time vigilant (s/min) | 4.5 ± 4.1 | 10.5 ± 4.4 | 22.92 | <0.001 |
| Pecking rate (no./min) | 10.9 ± 7.9 | 9.1 ± 5.9 | 0.42 | 0.518 |
| Net pecking rate (no./min) | 11.6 ± 8.2 | 11.2 ± 7.9 | 0.05 | 0.832 |

*Notes:* Net pecking rate was calculated discounting the time spent vigilant. Data are means ± 1 SD.

in arthropod counts. Instead, food availability depended mainly on individual tree characteristics that should be difficult for a flying bird to forecast from a distance prior to its arrival at any given particular trunk. Finally, the feeding success attained by focal birds did not differ between sunlit and shaded patches (0.8% variance explained by the effect of patch category (sunlit vs. shaded) on pecking rates).

On the other hand, differences in model temperature between locations in full sun and in the shade were highly predictable (82% of variance explained) and substantially large (difference of 14.6 ± 6.6°C, $\bar{x} = 1$ SD). Considering the equations that relate metabolic rate to environmental temperature in small passerines (Fig. 1A), the observed increase of operative temperatures at sunlit patches should allow birds to save up to ~45% of their thermoregulatory costs, a figure obtained using the average of regression parameters for *Parus* species in Kendeigh et al. (1977). This energy saving would become less important when $T_{\text{shade}}$ approaches the lower critical temperature, $T_{\text{lc}}$ (recall that the highest model temperatures recorded during the study period, roughly 33°C in full sun, were lower than the critical thermal maximum expected for small passerines; Calder and King 1974). Thus, the advantage of sun seeking should be higher under lower environmental temperatures.

We hypothesize that solar radiation should exert a striking influence on patch selection by treecreepers (and, ultimately, on their distribution and abundance) through its thermal effect on the bird's environment. For our three-year sample of birds, over 95% of the readings of $T_{\text{shade}}$ were below 21.5°C. This means that only rarely would some shaded locations fall within the thermoneutral zone. In this scenario, what is remarkable is not that the electivity of birds for sunlit patches was greater at lower temperatures, but that birds actively selected to forage in the shade at temperatures as low as ~6.5°C. These temperatures are well below the expected $T_{\text{lc}}$ for *Certhia brachydactyla* (21.5°C; Mozetich 1995) and, indeed, for most holarctic passerines in winter (Kendeigh et al. 1977). Assuming that water losses do not increase with temperature within the thermoneutral zone (Weathers and Greene 1998), the ''only metabolic benefits'' hypothesis predicts that, between lower and upper critical temperatures, the use of sun–shade patches should be proportional to their availability (i.e., electivity = 0; Fig. 1C). Alternatively, the ''trade-off with predation risk'' hypothesis predicts a shade-seeking behavior when tempertaure in the shade equals $T_{\text{lc}}$ (i.e., electivity $\sim -1$; Fig. 1F). Thus, the observed shade-seeking behavior rejects the ''only metabolic benefits'' hypothesis, because it reflects a cost to the use of sunlit trunks that must be large enough to counterbalance the energy savings afforded by sunlit patches.

Our results strongly suggest that this cost results from the increased risk of predation experienced by treecreepers while using sunlit patches. Four lines of evidence support this conclusion. First, results shown in Fig. 4 are consistent with the negative relationship between electivity for sunlit patches and $T_{\text{shade}}$ predicted by the ''trade-off with predation risk'' hypothesis. Second, our photogrammetric approach demonstrates that the image contrast and color discrepancy between bird mount and trunk background were more pronounced in full sun than in the shade. Third, such differences influenced the perceptual abilities of visually guided ''predators'': birds on sunlit patches were easier to detect by humans, and detection times were shorter in the sun. Finally, birds spent more time vigilant on sunlit patches, which confirms that they actually perceived a higher risk of being detected by potential predators.

Although predation risk may be traded off against the thermal quality of patches or habitats, there are relatively few studies that document such trade-offs (see review by Lima and Dill 1990). Grubb and Greenwald (1982), for instance, interpreted the patch selection patterns found in House Sparrows (*Passer domesticus*) as reflecting a compromise between the distance to cover that may represent a source of predators (farther is safer) and the energy savings afforded by cover (closer is warmer). Similar trade-offs between thermoregulation and predation risk have been postulated in lizards (J. A. Díaz 1992, Martín and López 1999), salamanders (Holomuzki 1986), and fish (Fischer et al. 1987).

Fig. 4 also shows that our data do not perfectly fit the predictions of the predation risk hypothesis, because treecreepers did not restrict themselves only to sunlit patches at temperatures below $T_{\text{lc}} - \Delta T$. In fact, the slope of the observed negative regression between electivity for sunlit patches and temperature was less steep than predicted. We can explain such discrepancy by considering that, in the early morning, when the sun is low and shadows are long, temperatures are low but there is a scarcity of trunk surfaces exposed to sunlight. This could increase the travel costs faced by treecreepers when flying to a sunlit trunk. Such interpretation is supported by the fact that the percentage of time spent flying by focal treecreepers was negatively correlated with $T_{\text{shade}}$ ($r = -0.476$, $P = 0.003$, $n = 36$), which suggests higher travel costs when electivity for sunlit patches is higher. An alternative explanation is that the increased length of flying times at low temperatures could reduce thermoregulatory costs (Webster and Weathers 1990).

In summary, we interpret the selection of shade as a behavioral mechanism for enhancing crypsis. Although treecreepers were difficult to detect because of their cryptic coloration, our results show that crypsis was much more effective in shaded patches than in sunlit ones. Increased detectability would force birds to ignore the thermal benefits of sun-exposed locations. Moreover, the selection for shaded sites, and thus crypsis enhancement, increased as the metabolic advantage of sun selection became smaller when operative temperatures approached $T_{lc}$. Thus, our results exemplify the importance of the predator detection subcomponent of risk (Lima and Dill 1990) not only in promoting the evolution of morphological adaptations, but also in shaping behavioral decisions that modulate the short-term effectiveness of crypsis (Bauwens and Thoen 1981, Dill and Fraser 1984).

In temperate latitudes during winter, possibilities for minimizing costs of thermoregulation by selecting sunlit patches are scarce because of the few clear days available. Geographical variation in winter cloudiness defines the background where the interactions that we have studied may be ecologically relevant for this species. Cloudiness varies strikingly with latitude, from 35–40% of the 9–10 h of winter daylight in southern Europe to 70% of less than 5 h of daylight at latitudes higher than 50–55° (W. Cramer, *personal communication*). Within this wide geographical range, many passerine species are winter residents in areas with high cloudiness (for example, the Brown Creeper *Certhia familiaris* at northern latitudes), which implies that cloudiness does not necessarily prevent winter residence. Therefore, the applicability of the thermoregulatory behaviors described in this paper cannot be generalized to any environmental condition or geographical location. They could play an important role favoring winter energy savings in southern latitudes of cold continental and/or montane climate, with low cloudiness and under windless conditions (Walsberg 1986, Wolf and Walsberg 1996). We also predict that such behaviors should be more important in species absent from high latitudes in winter, which tend to be less tolerant of cold stress than their northern counterparts. This is probably the case for the Short-toed Treecreeper, with a northern limit in its distribution range that does not reach 55°N (10–13° below the northern limit of *Certhia familiaris*). An interesting extension of this argument is that thermoregulation might play a prominent role in explaining the importance of southern mediterranean latitudes as winter quarters for many European species. Thus, the large winter densities of small passerines in mediterranean areas (Carrascal et al. 1998, Tellería et al. 1999) could also be explained by adding thermoregulation benefits to the food availability hypothesis, especially if wintering mediterranean populations are not limited by food availability.

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## LITERATURE CITED

Avery, M. I., and J. R. Krebs. 1984. Temperature and foraging success of great tits *Parus major* hunting for spiders. Ibis **126**:33–38.

Austin, G. T. 1976. Behavioral adaptations of the Verdin to the desert. Auk **93**:245–262.

Bakken, G. S. 1989. Arboreal perch properties and operative temperature experienced by small animals. Ecology **70**: 922–930.

Bakken, G. S., W. R. Santee, and D. J. Erskine. 1985. Operative and standard operative temperature: tools for thermal energetics studies. American Zoologist **25**:933–943.

Bauwens, D., and C. Thoen 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. Journal of Animal Ecology **50**:733–743.

Bednekoff, P. A., H. Biebach, and J. R. Krebs. 1994. Great Tit fat reserves under unpredictable temperatures. Journal of Avian Biology **25**:156–160.

Blem, C. R. 1990. Avian energy storage. Current Ornithology **7**:59–113.

Bouskila, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. Ecology **76**:165–178.

Calder, W. A., and J. R. King. 1974. Thermal and caloric relations of birds. Pages 259–413 *in* D. S. Farner and J. R. King, editors. Avian biology. Volume 4. Academic Press, New York, New York, USA.

Carlson, A., and J. Moreno. 1992. Cost of short flights in the Willow Tit measured with doubly-labeled water. Auk **109**:389–393.

Carmi-Winkler, N., A. A. Degen, and B. Pinshow. 1987. Seasonal time–energy budgets of free-living Chukars in the Negev Desert. Condor **89**:594–601.

Carrascal, L. M. 1987. Relaciones entre avifauna y estructura de la vegetación en el País Vasco atlántico. Dissertation. Universidad Complutense, Madrid, Spain.

Carrascal, L. M. 1988. Influencia de las condiciones ambientales sobre la organización de la comunidad de aves en un bosque subalpino mediterráneo. Doñana, Acta Vertebrata **15**:111–131.

Carrascal, L. M., P. Lopez, J. Martin, and A. Salvador. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. Ethology **92**:143–154.

Carrascal, L. M., J. Potti, and F. J. Sánchez-Aguado. 1987. Spatio-temporal organization of the bird communities in two Mediterranean montane forests. Holarctic Ecology **10**: 185–192.

Carrascal, L. M., J. C. Senar, I. Mozetich, F. Uribe, and J. Domenech. 1998. Interactions among environmental stress, body condition, nutritional status, and dominance in Great Tits. Auk **115**:727–738.

Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist **131**:271–290.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behavioral Ecology and Sociobiology **13**:205–209.

Cooper, R. J., and R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology **13**:29–37.

Cramp, S., and C. M. Perrins, editors. 1993. The birds of the Western Palearctic. Volume VII. Oxford University Press, London, UK.

De Jong, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of White-crowned Sparrows. Condor **78**:174–179.

Díaz, J. A. 1992. Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. Herpetologica **48**:293–300.

Díaz, M. 1992. Rodent seed predation in cereal crop areas of central Spain: effects of physiognomy, food availability, and predation risk. Ecography **15**:77–85.

Dill, L. M., and A. H. G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioral Ecology and Sociobiology **16**: 65–71.

Endler, J. A. 1987. Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Animal Behaviour **35**:1376–1385.

Fischer, R. U. Jr., E. A. Standora, and J. R. Spotila. 1987. Predator-induced changes in thermoregulation of bluegill, *Lepomis macrochirus*, from a thermally altered reservoir. Canadian Journal of Fisheries and Aquatic Sciences **44**: 1629–1634.

Grubb, T. C. Jr., and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. Animal Behaviour **30**:637–640.

Hagemeijer, W. J. M., and M. J. Blair, editors. 1997. The EBCC atlas of European breeding birds. Their distribution and abundance. Poyser, London, UK.

Hamilton, W. J., and F. Heppner. 1967. Radiant solar energy and the function of black homeotherm pigment. Science **155**:196–197.

Hedenström, A. 1992. Flight performance in relation to fuel load in birds. Journal of Theoretical Biology **158**:535–537.

Hogstad, O. 1988. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis **130**:45–56.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. Ecology **67**:737–748.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist **137**:91–115.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127–204 *in* J. Pinowski and S. C. Kendeigh, editors. Granivorous birds in ecosystems. Cambridge University Press, New York, New York, USA.

Kotler, B. P., Y. Ayal, and A. Subach. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia **100**:391–396.

Kotler, B. P., J. S. Brown, R. J. Smith, and W. O. Wirtz. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. Oikos **53**:145–152.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619–640.

Lustick, S., M. Adam, and A. Hinko. 1980. Interaction between posture, color, and the radiative heat load in birds. Science **208**:1052–1053.

Lustick, S., B. Battersby, and M. Kelty. 1978. Behavioral thermoregulation: orientation toward the sun in herring gulls. Science **200**:81–83.

Lustick, S., S. Talbot, and E. L. Fox. 1970. Absorption of radiant energy in Red-winged Blackbirds (*Agelaius phoeniceus*). Condor **72**:471–473.

Martín, J., and P. López. 1999. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. Oikos **84**:499–505.

Moreno, J., A. Carlson, and R. V. Alatalo. 1988. Winter energetics of coniferous forest tits, Paridae, in the north: the implications of body size. Functional Ecology **2**:163–170.

Mozetich, I. M. 1995. Ecología Invernal de Passeriformes en ambientes forestales mediterráneos. Dissertation. Universidad Autónoma, Madrid, Spain.

Ohmart, R. D., and R. C. Lasiewski. 1971. Roadrunners: energy conservation by hypothermia and absorption of sunlight. Science **172**:67–69.

Pianka, E. R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton University Press, Princeton, New Jersey, USA.

Repasky, R. R. 1991. Temperature and the northern distributions of wintering birds. Ecology **72**:2274–2285.

Root, T. 1988. Energy constraints on avian distributions and abundances. Ecology **69**:330–339.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Tatner, P., and D. M. Bryant. 1986. Flight cost of a small passerine measured using doubly labeled water: implications for energetics studies. Auk **103**:169–180.

Tellería, J. L., B. Asensio, and M. Díaz. 1999. Aves Ibéricas. Volume 2. Passeriformes. J. M. Reyero Editor, Madrid, Spain.

Vitt, L. J., and S. S. Sartorius. 1999. HOBOs, Tidbits and lizard models: the utility of electronic devices in field studies of ectotherm thermoregulation. Functional Ecology **13**: 670–674.

Walsberg, G. E. 1983. Avian ecological energetics. Pages 161–220 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian biology. Volume 7. Academic Press, New York, New York, USA.

Walsberg, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk **103**:1–7.

Watanuki, Y. 1986. Moonlight avoidance behavior in Leach's Storm-Petrels as a defense against Slaty-backed Gulls. Auk **103**:14–22.

Weathers, W. W., W. A. Buttemer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk **101**:459–472.

Weathers, W. W. and E. Greene. 1998. Thermoregulatory responses of Bridled and Juniper Titmice to high temperature. Condor **100**:365–372.

Webster, M. D., and W. W. Weathers. 1990. Heat produced as a by-product of foraging activity contributes to thermoregulation by Verdins, *Auriparus flaviceps*. Physiological Zoology **63**:777–794.

Wolf, B. O., and G. E. Walsberg. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology **77**:2228–2236.

Wolfe, J. L., and C. T. Summerlin. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. Animal Behaviour **37**:410–414.