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Abstract—By determining the microclimates that an animal experiences, habitats influence an animal's physiological capacities and ultimately its demographic and ecological performance. As a result, the ecology of organisms—especially of ectotherms—can be profoundly affected by the physiological consequences of habitat selection. Early ecologists such as Shelford and Chapman appreciated these issues, but most later ones tended to ignore physiology and instead focused on biotic interactions (e.g., competition). Recent technical and conceptual developments are now fostering a reintroduction of physiology into ecology. For issues relevant to thermal physiology, three steps are involved. First, the microclimates available in a habitat must be mapped. For ectotherms, this involves determining the operative environmental temperatures (T_e)—that is, the potential body temperatures available in a habitat. Biophysical techniques can now generate T_e maps with considerable accuracy. Second, the physiological effects of body temperature must be quantified. This requires laboratory studies of the effect of temperature on key performance traits. Third, the physiological suitability of habitats can be predicted by integrating the above environmental and physiological data. Analyses of the physiological consequences of habitat selection are exemplified in several case studies, and the importance of considering food and other factors in the analyses is stressed. An extension to endotherms is briefly discussed.

The study of how and why organisms select particular habitats has long been central to ecology. In fact, the early literature of ecology was often dominated by discussions of habitat associations. Of special interest in the early days of ecology was the concept of limiting factors: which physical factors (e.g., temperature, pH, salinity) limit the occurrence of organisms to particular habitats. Not surprisingly, early discussions often focused on interactions between physiology and the physical environment. Indeed, for many early ecologists, ecology and physiology were more or less synonomous concepts. Shelford, for example, defined ecology as "that branch of general physiology which deals with the organism as a whole . . . and which also considers the organism with particular reference to its usual environment" (1913, p. 1). Similarly, Chapman argued: "The interrelations of organisms in nature may be considered under the subject matter of ecology which is closely related to physiology, and in the minds of some biologists should be a subdivision of it" (1931, p. 3). Clearly, physiology was central to ecology at this time. In fact, physiological issues dominated nearly the first half of Chapman's (1931) book (*Animal Ecology*).

Beginning with Elton (1927), however, ecological studies began to shift their focus from analyses of physiologically mediated interactions between organisms and their physical environments to analyses of interactions between individuals or between species, in other words, to analyses of population and community

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phenomena. Elton himself knew that physiology should not be excluded from discussions of population and community issues; he nevertheless wrote: "Animals usually have appropriate psychological reactions by which they find a suitable habitat, so that . . . the ecologist does not need to concern himself very much with the physiological limits which animals can endure" (1927, p. 33). For the next half century or so, ecologists seem to have taken Elton's advice literally, for they did not in fact concern themselves much with physiology.

In recent years, however, many ecologists have seen the need to reincorporate physiology into ecology. Indeed, powerful mechanistic models have already clarified how dynamic fluctuations in the physical environment, via complex interactions with physiology (Porter et al. 1973; Christian et al. 1983; Kingsolver and Watt 1983; Porter and Tracy 1983; Christian and Tracy 1985) and morphology (Palumbi 1984; Denny et al. 1985), can dominate the behavior, life history, demography, and competitive interactions of animals (Levins 1968; Casey 1981; Heinrich 1981; Parsons 1983; Porter et al. 1983; Roughgarden et al. 1983; Stevenson 1983; Walsberg 1985; Beuchat and Ellner 1987; Dunham et al. 1989; Kingsolver 1989; Porter 1989; Spotila et al. 1989). For some organisms—particularly, small ectotherms (Stevenson 1985)—such environmental and physiological interactions can sometimes have a dramatic impact on population and community interactions.

My goal here is to expand on the argument that the physiological consequences of habitat selection are real and are ecologically important. Specifically, I argue that the habitat occupied by an animal, by determining microclimates that the animal experiences, influences the animal's physiological capacities and ultimately its ecological performance. I then build on this assumption by describing methods to quantify or map microclimates from an organism's perspective, to quantify the effects of microclimates on physiological performance, and to compare the physiological suitability of habitats by integrating the above environmental and physiological information. I then review a few case studies that document some ecological and demographic consequences of the interaction between habitat and physiology.

I largely restrict my remarks to the role of thermal biology in habitat selection by ectotherms (e.g., most insects, reptiles). Temperature is a key environmental variable, one that is physiologically significant as well as easily measured and manipulated. Relative to endotherms (birds, mammals, some insects), ectotherms are especially sensitive to environmental temperature (Porter and Gates 1969), and the thermal consequences of their habitat selection thus may be relatively conspicuous. Nevertheless, many of my remarks can be generalized to other "operational environmental" factors (e.g., water, nutrients; Mason and Langenheim 1957; Spomer 1973) and to other types of organisms. Therefore I conclude with a few general remarks about the physiological importance of habitat selection to endotherms.

Several recent papers have developed closely related themes. Grant (1988), Dunham et al. (1989), Kingsolver (1989), and Porter (1989) presented complementary perspectives of the physiologically mediated effects of the physical environment on growth, life history, and demography. Walsberg (1985) examined some

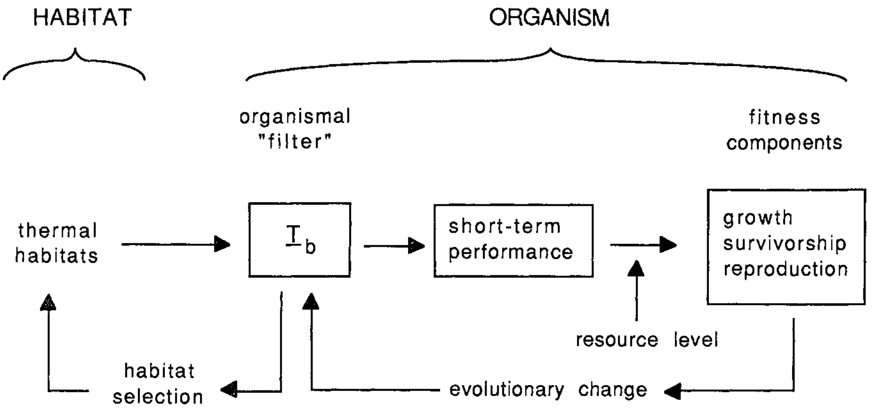


FIG. 1.—Influence of habitat selection on performance and fitness of ectotherms. By modifying the thermal regime of an organism, habitat selection influences an organism's fitness via its influences on T_b and thus on short-term physiological performance.

physiological (largely energetic) consequences of microhabitat selection in birds, and his comments are obviously relevant to mammals as well.

A CONCEPTUAL FRAMEWORK

A conceptual overview of how habitat selection influences physiological and ecological performance of ectotherms is shown in figure 1 (based on Huey 1982; Kingsolver and Watt 1983; Spotila and Standora 1985; Dunham et al. 1989). The macrohabitat selected by an animal determines the environmental thermal regime it experiences. However, most macrohabitats are thermally heterogeneous, and the actual body temperature (T_b) an animal achieves depends on its behavior (e.g., choice of microhabitat, activity level, posturing), its morphology (e.g., size, color), its physiology (e.g., metabolic rate, water loss), and sometimes even its manipulation of the environment (e.g., tent-making by caterpillars; Knapp and Casey 1986). Thus the organism's behavior, morphology, and physiology can be viewed as a filter that transduces the environmental thermal regime into a particular T_b (Kingsolver 1979; Tracy 1982; Kingsolver and Watt 1983). This T_b interacts with the ectotherm's physiology and morphology to influence its immediate ability to perform important behaviors (food gathering, social dominance, predator avoidance), which ultimately integrate to affect its long-term ability to grow, to survive, and to reproduce (Huey and Stevenson 1979; Heinrich 1981; Huey 1982; Knapp and Casey 1986; Dunham et al. 1989). Two feedback loops are important here: one short-term, the other long-term. The particular effect of T_b on the performance of an individual is modifiable by acclimatization (not shown in fig. 1; Levins 1968; Prosser 1986), and all organismal components are of course subject to evolutionary change (Levins 1968; Heinrich 1981; Huey and Kingsolver 1989).

An alternative but complementary perspective on the relationship between

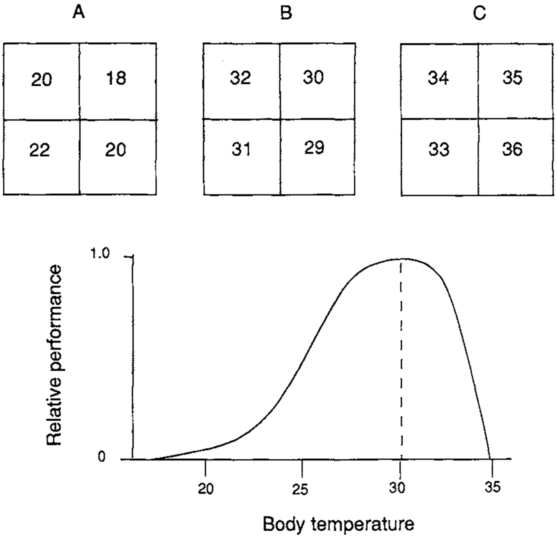


FIG. 2.—Physiological consequences of habitat selection for a hypothetical ectotherm. The top panels depict three habitats, each with four patches that differ in T_e (°C); the rightmost habitat is the warmest. The lower curve shows the effects of T_b on relative physiological performance (the dashed line at T_b = 30°C represents the optimal temperature). Judged by only thermal considerations, the average performance of this ectotherm will be best if it selects habitat B.

physiology and habitat selection views the thermal regime of a habitat or microhabitat as an environmental resource (see Magnuson et al. 1979; Mushinsky et al. 1980; Roughgarden et al. 1981; Tracy and Christian 1986). Thus, animals might compete for habitats with suitable basking sites or thermal refugia (Regal 1971; Beitinger and Fitzpatrick 1979) much the way they might compete for habitats with suitable food. If such sites are in short supply, competition for them could be intense, and nearby food resources could be depleted.

QUANTIFYING THE THERMAL QUALITY OF A HABITAT

The framework developed above can be made concrete by developing a quantitative index of the physiological quality (with respect to temperature) of a habitat. Two basic steps are involved (Porter et al. 1973; Huey and Slatkin 1976). One must first quantify the distribution of potential body temperatures available in a given habitat and then understand how those body temperatures influence relative physiological and ecological performance. A hypothetical example demonstrates the process (fig. 2).

Assume that the potential body temperatures of a given ectotherm are known for all points in the habitat. Then consider the three hypothetical habitats depicted in figure 2. Each habitat consists of four patches in which the ectotherm achieves a particular body temperature. An ectotherm in the leftmost habitat will be relatively cold, whereas one in the rightmost habitat will be relatively warm.

What does it mean ecologically for an animal to be "relatively cold" or "relatively warm"? Different species of ectotherms may differ greatly in their thermal optima and sensitivity (Bennett 1980); thus, different species may have quite different views of the relative thermal quality of a habitat. Accordingly, we need to develop methods that transduce the effect of particular body temperatures on ecologically relevant indices of organismal performance or (ultimately) fitness for each species (Huey and Stevenson 1979; Huey 1982, 1983; Hailey and Davies 1988). A start toward this goal can be accomplished by gathering data on the thermal dependence of whole-animal traits ("thermal performance curves") such as locomotor capacity, digestion rate, social dominance, feeding success, growth rate, or reproductive rate. For the hypothetical ectotherm in figure 2, 30°C is the "optimal" temperature.

By integrating these environmental and physiological data, one can rank habitats in terms of their physiological suitability. If one assumes that thermal physiology is the only relevant issue, then the middle habitat appears physiologically optimal. (Some complications will be evaluated below.)

IMPLEMENTING THE MODELS

Developing a Thermal Map of the Habitat

In applying this conceptual framework to specific systems, we need practical techniques of mapping the thermal environment from a given organism's perspective (Bakken and Gates 1975; Chappell 1983; Stevenson 1983; Grant 1988). As a first approximation, this can be done by specifying the potential equilibrium body temperature that an animal will achieve at every spot in its habitat. Such equilibrium body temperatures are usually called *operative environmental temperatures* and are abbreviated T_e (Bakken and Gates 1975; Robinson et al. 1976; Campbell 1977; Mahoney and King 1977; Roughgarden et al. 1981; Tracy 1982; Bakken 1989, 1991). These potential body temperatures provide a powerful way of conceptualizing a relevant thermal map of an animal's habitat (Roughgarden et al. 1983; Stevenson 1983; Waldschmidt and Tracy 1983; Grant and Dunham 1988; Grant 1990).

How can T_e be estimated? Unfortunately, T_e is usually poorly predicted from standard meteorological measures (e.g., shaded air temperatures at a height of 1 m). Indeed, T_e is a complex function of many factors, not just shaded air temperature. Equilibrium body temperatures depend not only on local environmental characteristics (e.g., wind speed, radiation load) but also on the particular heat-transfer properties (modified by color, shape, behavior; Casey 1981) and the activity of the organism itself. At any given spot at any given time, therefore, a single individual may have several T_e's, depending on its orientation, color, and activity level. Moreover, different animals in the same spot may have very different T_e's. For example, equilibrium body temperatures of a 1-g and of a 100-g ectotherm that have been exposed to identical environments can differ by as much as 10°C (Stevenson 1985).

In developing techniques to estimate the potential body temperatures of ectotherms, biophysical ecologists have made a major contribution to the study of habitat selection. They have developed two complementary techniques:

1. Detailed measures of key microclimate variables (e.g., solar radiation, wind speed, air temperature) can be taken over time and space, and these are combined with measures of relevant organismal properties (size, color, shape) in complex mathematical models that predict equilibrium and even transient body temperatures (Porter et al. 1973; Spotila et al. 1973; Gates 1980; Roughgarden et al. 1981, 1983; Tracy 1982; Waldschmidt and Tracy 1983).
2. Alternatively, one constructs hollow-body models (usually of copper) and then distributes these in the habitat (Bakken and Gates 1975; Stevenson 1983; Grant and Dunham 1988; Grant 1990; Bakken 1991). As long as the model approximates the size, shape, and spectral reflectivity of the organism, the model's internal temperature accurately estimates the equilibrium temperature of the ectotherm itself (assuming that evaporative cooling balances metabolic heat production). In effect these models physically integrate the heat-balance dynamics described by the formal mathematical models (Bakken and Gates 1975). (With some modifications, models can be used to predict environmental heat loads on endotherms; see below.)

These two approaches are complementary. The former approach enables one to understand the dynamics of heat flux as well as to predict T_e under hypothetical organismal or environmental conditions; however, it requires expensive micrometeorological equipment, and T_e must be computed. The latter approach requires relatively limited equipment and effort (exclusive of building models), provides instantaneous estimates of T_e, and yields superior spatial resolution (many models can be monitored simultaneously if a data logger is available). However, this "black-box" approach provides limited insight into the dynamics underlying T_e.

By sampling T_e at many randomly selected points, one can develop a thermal topographic map of a habitat (fig. 3), even in heterogeneous habitats (Christian et al. 1983; Roughgarden et al. 1983; Stevenson 1983; Waldschmidt and Tracy 1983; Christian and Tracy 1985; Grant and Dunham 1988; Huey et al. 1989; Grant 1990). This thermal map may change rapidly, of course, depending, for example, on clouds, wind, and incident radiation. Indeed, meteorological variation on a time scale of only 30–60 s can have important effects on T_b and flight activity of *Colias* butterflies (Kingsolver and Watt 1983; see also Dobkin 1985; below).

Quantifying the Thermal Dependence of Physiological Performance

The second step (fig. 2) in deriving a measure of the physiological quality of a habitat involves measuring the effect of particular body temperatures on physiological performance. Yet, what aspect(s) of physiological performance does one select? For organisms (e.g., bacteria) with fast generation times, population growth rate is probably the most ecologically relevant measure of physiological performance (see Charlesworth 1980). For most organisms, however, the thermal dependence of population growth rate cannot be measured. Alternatively, as emphasized by several workers (Bartholomew 1966; Huey and Stevenson 1979; Huey 1982; Arnold 1983), one should examine the effect of T_b on organismal-level performance (e.g., locomotor capacity, feeding success, sensory acuity, net en-

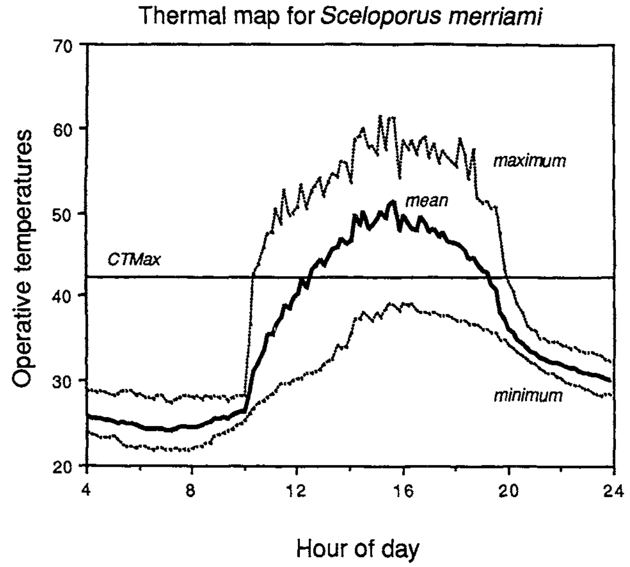


FIG. 3.—Operative temperatures available to the lizard *Sceloporus merriami* in the Grapevine Hills, Big Bend National Park, Tex. Sun hits this west face at about 1000 hours. *Solid curve,* mean T_e (from 45 models); *dotted lines,* maximum and minimum available T_e; *horizontal line,* CT_{max} (42.3°C). At midday, most of the ground surface is above the lethal temperature of the lizards. Unpublished data courtesy of B. W. Grant.

ergy availability) rather than on tissue or cellular-level processes (e.g., muscle-twitch velocity, enzyme activity). Of course, studies of lower-level physiological capacities are necessary for explaining the mechanistic bases of organismal performance, but such lower-level capacities are usually too removed from ecology to be direct predictors of ecological performance (Bartholomew 1966; Huey and Stevenson 1979; Pough 1989; but for counterexamples of lower-level indices accurately predicting organismal performance, see Garland 1984; Watt 1985; Koehn 1987; Powers 1987).

Once a relevant whole-organism function is selected, its thermal sensitivity can be measured. Then, after fitting a curve to the data (Huey 1982; Kingsolver 1989), one can specify relative performance (scaled 0–1) at any body temperature, the "optimal" temperature, or the "performance breadth" (the range over which an animal performs well; Levins 1968; Huey and Stevenson 1979). An example of the effect of T_b on various performance functions of a garter snake (*Thamnophis elegans*) is shown in figure 4 (from Stevenson et al. 1985; see also below).

This approach provides insight into the effects of temperature on the performance of ectotherms, but at the cost of physiological realism. In many species, the performance curve is not fixed but might shift with ontogenetic stage (Brett 1970), with acclimation (Levins 1968; Brett 1970; Prosser 1986) or physiological state (Pough 1989), or among individuals (Bennett 1987; Lynch and Gabriel 1987; Huey and Kingsolver 1989). Moreover, different physiological functions sometimes vary in their thermal sensitivities (see, e.g., fig. 4), and different physiologi-

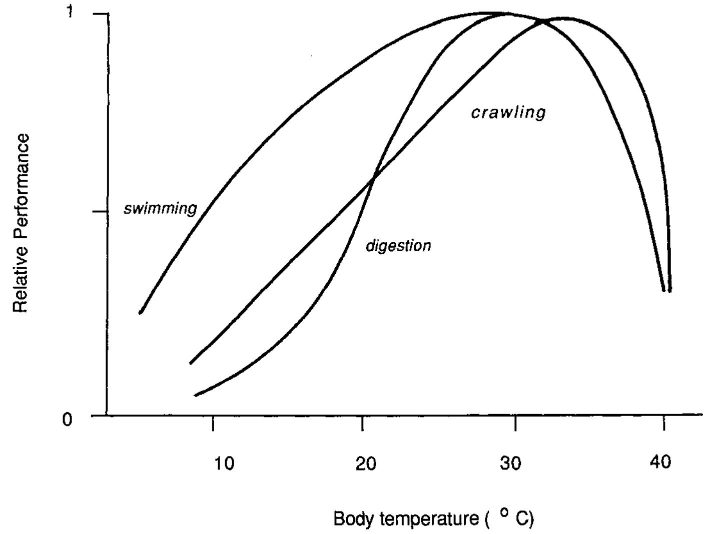


FIG. 4.—Relative performance (crawling speed, swimming speed, digestion rate) of the garter snake (*Thamnophis elegans*) as a function of body temperature. Redrawn from Stevenson et al. 1985.

cal activities may have fundamentally unique currencies and may operate and produce feedback over different time scales (B. W. Grant, personal communication). These considerations obviously complicate the evaluation of the physiological significance of particular T_b (Huey 1982), but some progress has been made to deal with these complications (McFarland 1976; Crowder and Magnuson 1983; Beuchat and Ellner 1987; see below).

The ecological context also influences organismal performance. For example, the physical structure of the habitat alters locomotor performance (Huey and Hertz 1984; Losos and Sinervo 1989), and behavior in the laboratory may differ from that in the field (Huey 1982; Webb 1986; Pough 1989). Predators or competitors can affect performance and habitat quality (Huey 1982; Roughgarden et al. 1983). Moreover, both environmental (resource) productivity and environmental thermal regimes interactively affect performance in nature. Brett's (1971) study of the thermal dependence of growth in fish provides an instructive example. On unlimited rations, fish grew fastest at about 15°C; but at progressively reduced food rations, fish grew fastest at progressively lower temperatures. (The shift in the optimum for growth reflects an interaction between the effects of T_b on processing and on metabolism [recall that resting metabolic rate increases exponentially with T_b]. When T_b is high but food ration is low, the net energy available for growth is low.) Obviously, growth rate—a performance measure—depends in nature not only on the potential body temperatures available but also on environmental resources and on interactions with other organisms (Stevenson 1983; Dunham et al. 1989). I return to this important issue below.

Predicting Habitat Quality

We can now combine our data about the distribution of potential body temperatures with our data about the thermal dependence of performance to develop explicit indices of the physiological suitability of various habitats. To date these indices are rather crude, but they are a start.

Huey and Slatkin (1976) developed a model that explored the energetic costs and benefits of various degrees of thermoregulation by ectotherms. Their model is relevant to general discussions of habitat selection because it identifies two important ways in which habitat influences net physiological benefits. (1) By determining the *frequency* distribution of potential body temperatures and environmental productivity, a habitat influences the potential energy gain of an ectotherm. (2) By determining the *spatial* distribution of those potential body temperatures, a habitat influences the energetic costs associated with thermoregulatory movements: A habitat in which thermoregulation is difficult should reduce its physiological suitability. This hypothesis is supported by field observations (Huey 1974; Lee 1980) and especially by a clever experiment (Withers and Campbell 1985). By altering the duration of thermal reinforcement in a thermal shuttle box, Withers and Campbell (1985) modified the costs of thermoregulation to desert iguanas (*Dipsosaurus*). When the thermal reinforcements were reduced, thereby increasing the habitat-induced cost of thermoregulating, the iguanas regulated at a lower and less precise T_b.

Tracy and Christian (1986) developed an index of home-range quality, whereby quality is influenced both by the availability of various body temperatures and by the physiological effects of temperature on performance. Formally, their index is

$$I = \int_{t=0}^{24\text{ h}} \int_{T_b = CT_{\min}}^{CT_{\max}} A(T_b, t) P(T_b)\, dT_b\, dt \,, \tag{1}$$

where I, the product of area (m^2) and time (h), is a "spatiotemporal index of the benefit derived from a home range" (Tracy and Christian 1986, p. 611); $P(T_b)$ is the performance (0 to 1) of an animal at a given T_b relative to the animal's performance at its optimal T_b; $A(T_{b,}\, t)$, which is measured in square meters, is the total area in the home range in which the animal can achieve a particular T_b at a particular time t; and $CT_{\max}$ and $CT_{\min}$ are the critical thermal maximum and minimum, respectively.

These two models have limitations. The model of Huey and Slatkin (1976) incorporates information on physiology, resource productivity, and the cost of thermoregulation, but its terms are not readily measurable. Thus, the model is only conceptual, and its predictions are qualitative at best. The Tracy and Christian (1986) model does not have this limitation, yet it ignores thermoregulatory costs (i.e., the spatial distribution of T_e) and environmental productivity, and it assumes that only a single T_e is associated with each spot at a given time (Bakken 1991). An additional weakness of the index is that it is a function of area (home-range size): Because I increases with home-range size (A), different-sized lizards (which may have different-sized home ranges) will have different values of I, even if the thermal qualities of their home ranges are identical (B. W. Grant, personal communication). Moreover, 24 h (see eq. [1]) may be an inappropriate time frame for analysis (Dunham et al. 1989).

Grant (1988, personal communication) solved some spatial problems of the model of Tracy and Christian (1986) by making the index of home-range quality unitless. This can be done by randomly placing an array of models in an animal's home range and then calculating the fraction of the available home range (percentage of models) with T_e that is within some ecologically relevant interval of T_b (e.g., optimal temperature range, above-lethal temperatures). Grant explicitly did not integrate over time and thus developed an instantaneous index of habitat quality. Grant's approach enables one to quantify at each instant both thermal constraints (e.g., the fraction of the home range too hot or too cold for survival) and the thermal opportunities (e.g., what fraction of the home range is thermally optimal for a specified physiological process) of a habitat. Nevertheless, this approach still assumes that the spatial pattern of T_e is relatively unimportant, which is probably valid in habitats where thermal heterogeneity is fine-scaled relative to home-range size but is inappropriate for habitats with coarse-grained thermal heterogeneity (van Berkum et al. 1986). It also ignores resource levels.

Despite these limitations, the models discussed above have provided some insight into the physiological consequences of habitat selection in ectotherms. Refinement of these models (see also Bakken 1991) requires the inclusion of stochastic and risk elements (Kingsolver and Watt 1983), the explicit treatment of (1) how habitat quality is influenced by the spatial and temporal distribution of T_e (Withers and Campbell 1985; Dunham et al. 1989) as well as by environmental productivity (see below) and of (2) the difficult issues of multiple physiological optima and of conflicting physiological goals (McFarland 1976; Crowder and Magnuson 1983; Beuchat and Ellner 1987; Huey et al. 1989). Ultimately, the models must be expanded to predict how demography is influenced by the physiological consequences of habitat selection. Progress has already been made in this direction (Riechert and Tracy 1975; Beuchat and Ellner 1987; Dunham et al. 1989; Kingsolver 1989; Porter 1989).

CASE STUDIES

I now describe several case studies that demonstrate various physiological or ecological consequences to ectotherms of habitat selection. Several of these studies predict aspects of the fitness of organisms in various thermal habitats.

Oviposition-Site Selection in Drosophila

Most adult organisms are mobile and can thus readily change habitats or microhabitats if local microclimate conditions are physiologically unsuitable. Some developmental stages (eggs in particular) do not have this option. Therefore, females looking for suitable oviposition sites should pay careful attention to physical conditions, especially given that animals early in development are notoriously intolerant of extreme temperatures (Brett 1970; Muth 1980).

An example of a thermally governed shift in habitat selection comes from a recent study of *Drosophila melanogaster* (Jones et al. 1987). Because development of *D. melanogaster* is optimal over only a narrow range of body temperatures, eggs developing at low elevation might overheat, whereas those developing at high elevation might not get hot enough. The impact of altitudinal variation in microclimate on developing flies could, however, be ameliorated if females partially based their oviposition-site selection on the thermal properties of those sites. For example, females should oviposit in relatively warm sites at high elevation.

Because locating oviposition sites of *Drosophila* is notoriously difficult, Jones et al. (1987) used an indirect approach to determine whether oviposition-site (habitat) selection might reflect thermoregulatory considerations. They exploited a temperature-sensitive eye mutation in which adult eye color of *Drosophila* depends on developmental temperatures experienced by early pupae (e.g., cold-reared pupae have dark eyes as adults). They introduced mutant adults at a low- and at a high-altitude site, and they later captured offspring and scored their presumed pupal-thermal regime.

After calibrating the eye-color index against known thermal regimes of laboratory flies, Jones et al. (1987) found that the (estimated) developmental temperatures for pupae from the two populations were rather similar given the differences in average air temperatures for the two altitudes. Consequently, females appear to oviposit in relatively warm microenvironments, especially in the montane site. Jones et al. (1987) argued that the flies may use thermoregulatory cues to select oviposition sites and that they do so because of physiological considerations. Further work will be necessary to determine whether the thermal environment at time of oviposition is a good predictor of future thermal environments and whether females are in fact ovipositing nonrandomly with respect to available oviposition sites.

Oviposition-Site Selection in Mosquitoes

In a pioneering study, Kingsolver (1979) examined the physiological, developmental, and demographic consequences of oviposition-site selection by female pitcher plant mosquitoes (*Wyeomyia smithii*). He was particularly interested in the demographic consequences of ovipositing on pitcher plants in sun versus those in shade.

Wyeomyia spend their egg, larval, and pupal stages in the fluid-filled pitchers of the northern pitcher plant (*Sarracenia purpurea*). Developing mosquitoes experience very different thermal environments (and hence have different development rates), depending on whether the pitcher plant selected by their mother is in shade or in sun.

Kingsolver (1979) used energy balance equations and field microclimate measurements to predict temporal patterns of T_e in both shaded and sunny pitcher plants. (His model predicted pitcher temperatures to within 2°–3°C.) He also monitored the effects of temperature on developmental rates in the laboratory.

Using simulation analyses, Kingsolver (1979) predicted that oviposition-site selection should have profound demographic consequences. Eggs and larvae develop slowly in shaded pitcher plants, such that most larvae will be forced to diapause after only one generation. In contrast, eggs and larvae develop rapidly in pitcher plants in sun, such that two generations can be completed before diapause is required. Interestingly, the obvious demographic advantage of ovipositing in pitcher plants in sun is partially offset: Because pitcher plants in sun sometimes desiccate, the probability of larval death there is relatively high and variable.

Habitat Selection in Hummingbird Flower Mites

Dobkin (1985) analyzed the consequences of habitat selection by hummingbird flower mites in Trinidad. These nectarivorous mites inhabit and breed in fluid-containing inflorescences of *Heliconia*. If the microclimate of a given inflorescence is unsuitable, the mites are able to disperse only by climbing onto the bill of a visiting hummingbird and then hitching a ride in the bird's nares to another inflorescence.

Bract temperatures increase rapidly when a sun fleck illuminates the bract, even if only for a few minutes. Such transient overheating reduces reproductive success and probably the survival of mites introduced experimentally into sunny inflorescences. Not surprisingly, the distribution of mites suggests that mites seem to avoid poorly shaded inflorescences.

This is an interesting problem of habitat selection, for a mite arriving at an inflorescence has only seconds to evaluate the suitability of the inflorescence. Because the bracts are shaded most of the time, immediate thermal cues are unreliable cues of daily insolation patterns, except in rare instances when the mite arrives at an illuminated bract. A mite making an incorrect decision may not survive unless another hummingbird soon provides an escape route. Conspecific cuing (Kiester 1979)—that is, using the presence and absence of conspecifics as an indicator of the long-term thermal suitability of a bract—might help.

Retreat-Site Selection in Garter Snakes

Many active ectotherms carefully regulate body temperatures by moving between warm and cold microenvironments. Nevertheless, no ectotherm is always active, and most actually spend very long periods in retreats (Huey 1982). Ectotherms in retreats may find that thermoregulatory opportunities are very different from those available when they are exposed on the ground surface. Consequently, retreat-site selection may have a profound impact on an ectotherm's thermal physiology and ecology.

My colleagues and I (Huey et al. 1989) recently completed a study of the physiological consequences of retreat-site selection in garter snakes near Eagle Lake, California. Garter snakes (*Thamnophis elegans*) spend long periods—sometimes several consecutive days, even in good weather—in retreats (usually under rocks). The rocks available to garter snakes vary from small rock flakes to huge boulders.

To determine whether garter snakes select rocks with respect to the thermal properties of the rocks, we monitored the T_e under a series of rocks differing in size and shape for 24 h during midsummer. The rocks were distributed in a geometric grid (called "Snakehenge") on a south-facing and open slope.

Representative plots of the range of T_e available to snakes under rocks are shown in figure 5. Also indicated are the critical thermal limits (upper and lower T_b at which the righting response is lost) of the snakes as well as the preferred temperature range (28°–32°C, the body temperature selected in laboratory thermal gradients) of the snakes. The critical thermal limits set approximate bounds on the range of temperatures in which snakes survive, whereas the preferred temperature range often specifies temperatures that maximize physiological performance (fig. 4; Huey 1982).

The magnitude of the daily thermal cycles beneath the rocks are strongly influenced by rock thickness. Thermal cycles were most variable under thin rocks (fig. 5*a*): T_e exceeded the critical thermal maximum of snakes by day and dropped to near the critical thermal minimum at night. Thermal cycles were least variable under thick rocks (fig. 5*a*), but available T_e's were low and in fact never reached the preferred range of the snakes. Thermal cycles were moderately variable under medium-thickness rocks (20–40 cm; fig. 5*b*), and available T_e's were often within the preferred range.

To evaluate the physiological consequences of selecting rocks of different thicknesses, we analyzed retreat-site selection with respect to several possible thermoregulatory needs, four of which are summarized here as examples. Our calculations are based on one constraint: the snakes were not allowed to change (or leave) retreat sites.

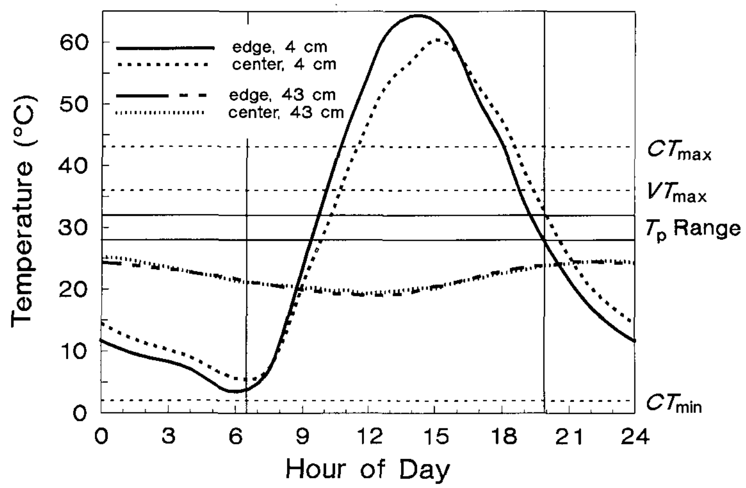
1. Using the T_e data, we calculated whether a snake staying under a given rock would overheat at some time during the 24-h day. During the afternoon at Eagle Lake, snakes selecting thin rocks (i.e., less than 20 cm) in sun would overheat and die (fig. 6*a*). Indeed, to avoid experiencing T_b above their voluntary maximum (36°C), snakes would have to select rocks at least 22 cm thick. Because almost a third of the rocks at Eagle Lake are small ($<$ 20 cm), the risk of overheating would be substantial if snakes selected rocks at random with respect to size.

2. We estimated the cumulative time during the 24-h day that snakes could achieve T_b within the preferred range. As noted above, a variety of physiological functions of garter snakes (fig. 4) are maximal within or near the preferred temperature range (28°–32°C), and thus overall ecological performance might be maximized by spending long periods within this range. Our calculations suggest that snakes can maximize time in this range (in midsummer) by retreating under rocks around 30 cm thick. In fact, a snake spending all day under a 30-cm rock can probably maintain T_b within the preferred range for nearly 20 h. This is nearly as well (22.2 h) as a snake (a ''Panglossy''snake, not shown) able to move at will to any available microhabitat.

3. We estimated the net energy availability to a snake that was digesting food (see below), as well as the energy losses of a fasting snake. A snake that is maximizing net energy availability should seek temperatures near 29°C, whereas one attempting to minimize energy losses should select temperatures as low as possible. Accordingly, one would expect snakes exemplifying these two extremes to use quite different retreat sites.

Snakes with food could maximize net energy availability by retreating under rocks 25–30 cm or by moving within a burrow at least 15 cm deep (fig. 6*c*). Surprisingly, fasting snakes could minimize energy expenditures in many of the

a) Thin and Thick Rock Temperatures



b) Medium Thickness Rock Temperatures

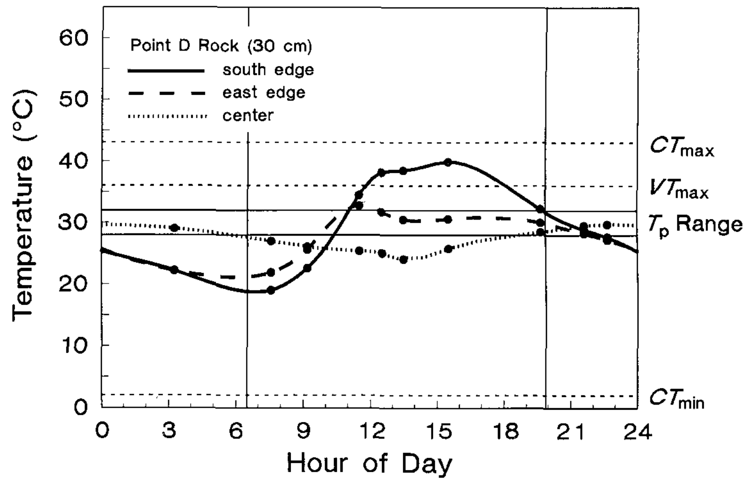


FIG. 5.—Daily cycles of temperatures available to garter snakes at Snakehenge, Eagle Lake, Calif. Also plotted are the CT_{max} and CT_{min} (upper and lower temperatures at which the righting response is lost), VT_{max} (voluntary maximum temperature), and T_p range (preferred temperature range). *a*, Temperatures available under a thick and thin rock. Edge and center temperatures, which delimit the range of available temperatures, are shown. Snakes would die of heat stress at midday under thin rocks but would never reach T_p levels under thick rocks. *b*, Temperatures under a rock of intermediate thickness. Snakes could achieve T_p for much of the day. Redrawn from Huey et al. 1989.

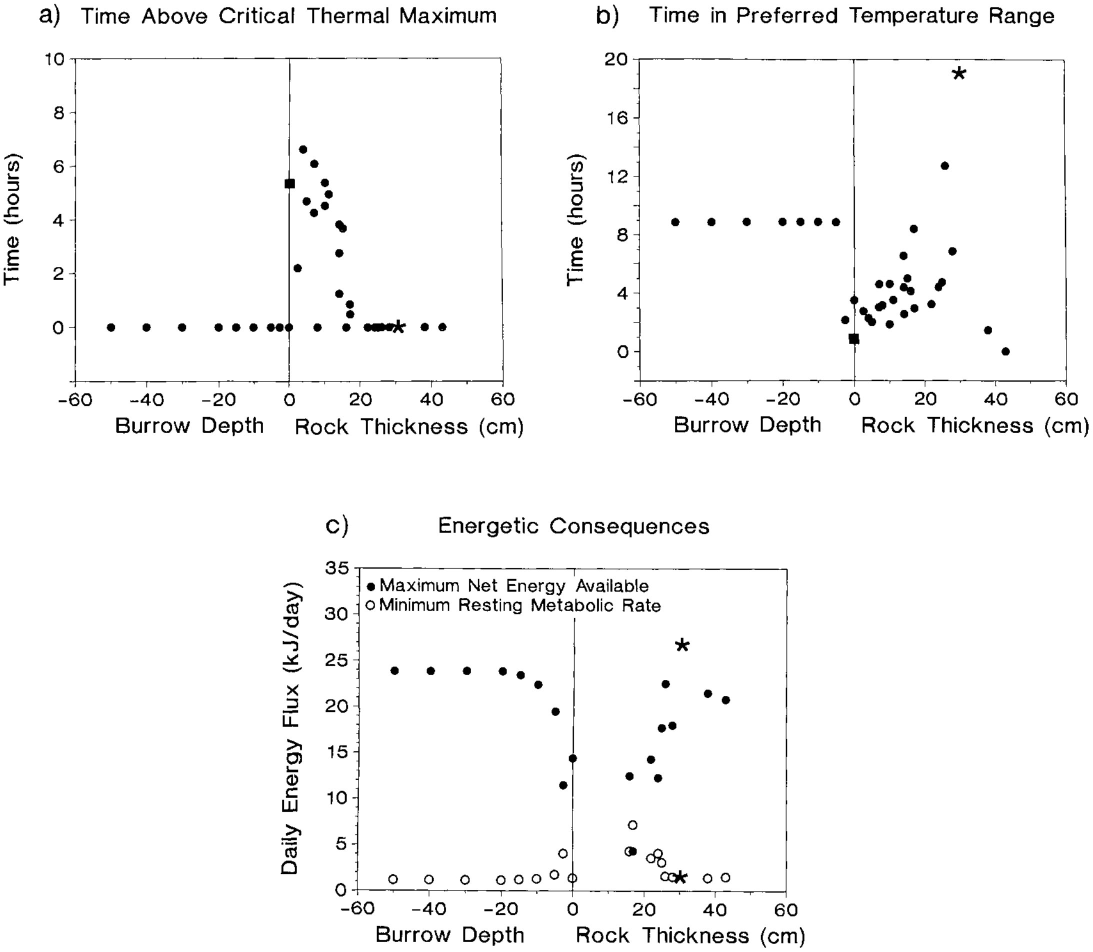


FIG. 6.—Consequences of retreat-site selection to garter snakes. *a,* Cumulative time (over 24 h) during which temperatures under rocks of different heights or in burrows at different depths exceed the snake's $CT_{\max}$ (43°C). *Asterisk,* value for the rock shown in fig. 5*b*; *square,* value for a snake on the open ground; *filled circle at 0 rock thickness,* value for a snake on shaded ground. *b,* Cumulative time when at least part of the thermal gradient under a rock (or down a burrow) in which a snake could achieve preferred temperatures (28°–32°C). *c,* Estimated energy consequences of retreat-site selection. *Open symbols,* minimum daily resting metabolic flux (kJ/d) for a 100-g snake as a function of retreat site. *Solid symbols,* maximum net energy available. Excluded are retreats that exceeded the snake's $CT_{\max}$ at some time of day. Redrawn from Huey et al. 1989.

same places (rocks $>$ 25 cm thick, fig. 6*c*). However, snakes could have even lower metabolic rates if they used thin rocks at night and thick ones by day.

The marked thermal differences among rocks obviously present garter snakes with varied themoregulatory opportunities, and in general rocks around 30 cm thick seem to be optimal for several physiological functions (Stevenson et al. 1985; fig. 4), even ones that a priori might seem in conflict (e.g., maximizing net energy availability vs. minimizing energetic expenditures). Do snakes select microhabitats with respect to those opportunities? Descriptive field evidence suggests that they do. Indeed, snakes usually use rocks 20–40 cm in diameter and conspicuously avoid small rocks, which are abundant but which get very hot by day.

This study shows that retreat-site selection can have a profound effect on a snake's potential body temperatures and in turn on its thermal physiology. Many retreat sites are lethal to the snakes at least at some times of day, whereas other sites enable snakes to achieve temperatures in the preferred range or to maximize net energy availability for long periods. Retreat-site selection is only one aspect of habitat selection by garter snakes. However, because these snakes spend far more time in retreats than in aboveground activity, physiological consequences associated with various retreat sites may be key factors in overall habitat selection by snakes.

MULTIPLE DIMENSIONS OF HABITATS

The above examples illustrate some physiological consequences of habitat selection based solely on a single dimension, the thermal environment. I have tried to show examples of how considering this single niche dimension can often help us predict the temporal and spatial patterns of habitat use in animals. However, the ecological performance of an animal depends on many factors in the environment, not just on operative temperatures and not just on its thermal physiology. Environmental productivity, parasites, predators, competitors, and irritants all potentially interact with physiology; models of habitat selection need to incorporate these complex interactions (Huey 1982; Stevenson 1983; Dunham et al. 1989). However, some progress has already been made with respect to interactions between food and temperature.

The joint importance of food and environmental temperature is clearly shown in a classic study by Riechert and Tracy (1975) on a web-building spider (*Agelenopsis*). They studied the energy budgets of spiders in several microhabitats that differed in thermal regimes and in food availability. Three of these microhabitats are compared in table 1. Spiders in the two grassland microhabitats (one with full shade, one with partial shade) had slightly higher food-capture rates (per hour of activity) than did spiders in a nearby lava-bed surface habitat (no shade). However, spiders in the grassland microhabitats that afforded full shade could be active for much longer than could spiders in either of the other two microhabitats. As a consequence, predicted offspring production was greatest for spiders at the shaded grassland sites.

In subsequent studies, Riechert has shown that spider densities are highest in

TABLE 1

CONSEQUENCES OF HABITAT SELECTION BY *AGELENOPSIS*

CONSEQUENCE	HABITAT Grassland (Full Shade)	 Grassland (Partial Shade)	 Lava (No Shade)
Available prey dry mass (mg/h)*	4.7	4.5	1.9
Prey capture rate (mg/h)*	2.8	2.7	1.1
Activity period (h)	12.7	8.7	4.3
Total prey consumed (mg/d)	23.8	15.7	3.2
Predicted offspring	415	273	54

NOTE.—Data from Riechert and Tracy 1975.
* Per hour of spider activity.

the shaded areas (Riechert 1981), that spiders select habitats (in part) on the basis of thermal properties (Riechert 1985), and that spiders will fight for sites with optimal thermal qualities (Hammerstein and Riechert 1988). The thermal factors of a habitat, by determining activity times, have a major impact on the behavior and ecology of these spiders.

Habitat selection can sometimes reflect a conflict between food availability and thermal stress. Swingland (1983) reviewed a dramatic example from his collaborative work on the giant Aldabra tortoise (*Geochelone gigantea*). Some individual tortoises migrate near the beginning of the rainy season from habitats in the interior of the island to those near the coast (Swingland and Lessells 1979). These migrating tortoises gain access to extra food, and such females have relatively high reproductive output. However, because little shade is available during the journey to the coast, some tortoises die of heat stress during migration. The advantages and risks of habitat selection in these tortoises are obviously complex (Swingland 1983).

Crowder and Magnuson (1983) modeled how habitat selection by fish relates to temperature and to food resources. They were particularly interested in the bioenergetic interactions between temperature and food on potential growth rates. Using a bioenergetic model developed by Kitchell et al. (1977), Crowder and Magnuson (1983) simulated potential growth rates of fishes among habitats in which temperature and food availability varied individually and then in concert. Fishes selecting habitat on the basis of bioenergetic interactions between food and temperature should grow faster than those selecting habitat on the basis of food alone or on temperature alone.

Many aquatic animals make daily vertical migrations into warm shallow waters at night. Such daily habitat shifts maximize net energy gain in a larval sculpin (Wurtsbaugh and Neverman 1988).

The insights of Brett (1970), Riechert and Tracy (1975), Swingland and Lessells (1979), Crowder and Magnuson (1983), and Dunham et al. (1989) have significant implications for models of habitat selection based strictly on optimal-foraging considerations. Net energy gain (and hence growth and reproduction) and even survival depend not only on food levels but also on the thermal environment. An

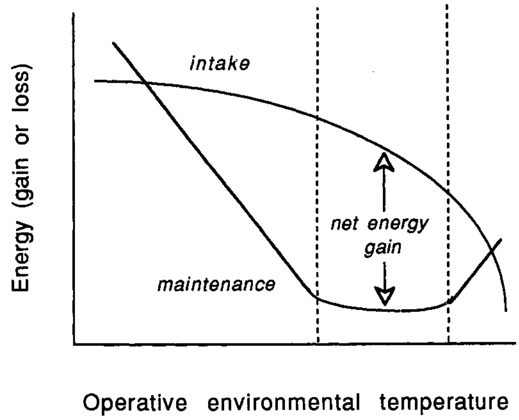


FIG. 7.—Effects of operative environmental temperatures on energetics of endotherms. Maintenance metabolic expenses and energy gained from food intake are plotted. Net energy gain, the difference between energy gain and loss, is maximal at temperatures within the thermal neutral zone (delimited by dashed lines). Redrawn from Ames 1980.

inevitable and important consequence is simply this: net energy gain is sometimes maximized by selecting patches that are "suboptimal" with respect to food density.

EXTENSION TO ENDOTHERMS

The concepts developed here must be modified for endotherms (e.g., birds, mammals, some insects). For example, the concept of a thermal performance curve (fig. 2) is obviously inapplicable to most endotherms because these animals usually maintain a relatively constant body temperature. Nevertheless, environmental thermal regimes may still have profound impacts on the behavior, ecology, and even distributions (Root 1989) of endotherms. Extreme temperatures in some habitats can cause stress and even death (Salzman 1982). Moreover, metabolic expenditures of endotherms are high and are strongly influenced by environmental temperature: resting metabolic rates are lowest at ambient temperatures within the animal's thermal neutral zone and increase with temperatures outside that zone. Because food intake of endotherms is often inversely related to environmental temperatures, net energy gain—the discretionary energy available for activities such as behavior, growth, and reproduction—is often maximal at intermediate environmental temperatures (Ames 1980; fig. 7). Accordingly, studies of the physiological consequences of thermal habitat selection to endotherms focus on how thermal regimes influence energy budgets (Ames 1980; Walsberg 1985) or survival (Austin 1976; Salzman 1982). Numerous studies have documented important effects of the thermal environment on behavior, time budgets, and energetics of endotherms (Ricklefs and Hainsworth 1968; Moen 1973; DeWoskin 1980; Chappell and Bartholomew 1981; Avery and Krebs 1984; Bennett et al. 1984; Belovsky and Slade 1986). Studies of the physiological consequences of microhabitat selection in birds have recently been reviewed by Walsberg (1985).

Before giving some brief examples of the physiological consequences to endotherms of habitat selection, I must first mention how the concept of an operative environmental temperature (T_e) must be modified for endotherms. Two special traits of endotherms have important influences on heat transfer (Bakken 1976, 1980; Robinson et al. 1976; Mahoney and King 1977). First, their insulation (fur, feathers) significantly complicates analyses of heat transfer (Walsberg et al. 1978; Walsberg 1988*a*, 1988*b*). Second, their high body temperature means that their energy budgets are strongly influenced by wind chill in a cold environment (Buttemer et al. 1986). Consider a bird in a cold, windy habitat versus the same bird in a cold, windless habitat. The T_e might be the same in either habitat, especially if radiant heating is minimal (e.g., if there are cloudy skies), but the bird in the windy habitat will need to expend much more energy in maintaining a normal body temperature.

To modify the concept of operative temperature so that it indexes heat flux, biophysical ecologists refer to "standard operative temperature" (T_{es}; Bakken et al. 1985; Bakken 1991). This thermal index permits direct comparisons of the thermal stress to endotherms imposed by their microenvironments (Bakken 1976). The T_{es} can be estimated from calibrated, heated taxidermic mounts (heat production can be inferred by monitoring the electrical power necessary to maintain a mount temperature equivalent to that of the endotherm under study; Bakken et al. 1985), where the copper mounts are covered with the animal's integument, or from simultaneous measurements of T_e and wind speed (Chappell and Bartholomew 1981; Bakken et al. 1985; Greek et al. 1989). (Note that for some studies, however, simple painted spheres may be adequate [Walsberg and Weathers 1986].)

Because the primary focus of this paper is ectotherms, I cite only a few examples dealing with endotherms (see also Bakken 1991). Some of the most conspicuous examples of the physiological consequences of habitat selection come from studies during winter. This can be an energetically stressful time for endotherms: short photoperiods restrict foraging times, and cold days and nights increase metabolic requirements (fig. 7). Many small (< 35 g) passerines begin their nocturnal fasts with fat reserves adequate to keep them alive only for one night plus part of the following day (King 1972; Buttemer 1985).

Selection of roost sites often reflects thermoregulatory considerations, especially for small birds in winter (Buttemer 1985; Walsberg 1985). Birds roosting in sheltered sites (cavities or domed nests) can reduce nocturnal power expenditures by nearly one-half (Walsberg 1985, table 3; Buttemer et al. 1987), primarily because convective heat loss is greatly reduced (Walsberg 1985). American goldfinches in Michigan save considerable energy by restricting their midwinter roost sites to the leeward side of trees with especially dense needles (Buttemer 1985). An Andean hummingbird shifts from exposed roost sites in summer to more protected ones in winter (Carpenter 1976).

Low temperatures and short days in winter also influence foraging intensity and social interactions of birds. In particular, small birds must forage intensively just to meet maintenance and thermostatic requirements (Gibb 1954). For example, chipping sparrows in midwinter spend 95% of the day foraging, and they find and consume a seed every 1–2 s (Pulliam and Parker 1979). Yellow-eyed juncos (Caraco 1979) during winter spend much more time feeding (75%) on cold days ($T_a < 9°C$) than on warm days (55%; $T_a > 19°C$). Interestingly, juncos spend less time in aggression (laboratory and field experiments) on cold days (Pulliam et al. 1974), presumably because the low ambient temperatures increase metabolic demands such that feeding takes priority over aggression. When Caraco (1979) supplemented food supplies on cold days, the birds increased aggressive levels.

Microclimates also influence selection of nesting sites. Hummingbirds in the Rocky Mountains use nest sites that reduce heat loss at night and in the early morning (Calder 1973). Warbling vireos in Arizona select nest sites that are shielded from the hot afternoon sun, thereby reducing heat stress (Walsberg 1981).

The major effects of environmental temperatures on the energy budgets of endotherms can potentially be exploited in behavioral experiments (see, e.g., Caraco 1979). Consider a laboratory behavioral study (e.g., optimal foraging) in which it is important to manipulate costs and benefits associated with a particular behavior, food, or ''habitat.'' One way to manipulate ''costs'' is simply to manipulate environmental temperatures in the laboratory (T_{es}, fig. 7). The elegance of this manipulation is that ''all else'' (e.g., food quality, spatial distribution of food) can be kept constant across trials. Caraco et al. (1990) have recently implemented this manipulation in studies of foraging choice in birds.

CONCLUDING REMARKS

My intent has been to show that physiological considerations should play a significant role in analyses of habitat selection (or of many areas of behavioral, population, and community ecology). To me, the attraction of this field is the opportunity to explore mechanistic and physiological links between the physical environment and ecology. The field is at a formative stage, and much remains unexplored. Nevertheless, the central questions at issue are important: How and to what extent do the physical environment and physiology jointly influence behavior, predation, competition, social dominance, life history, demography, and population regulation?

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SELECCIÓN DE HÁBITAT DE NIDIFICACIÓN POR EL BÚHO REAL *BUBO BUBO* EN AMBIENTES MEDITERRÁNEOS SEMIÁRIDOS

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RESUMEN.—*Selección de hábitat de nidificación por el Búho Real* Bubo bubo *en ambientes mediterráneos semiáridos*. Se han estudiado los factores que influyen en la selección de hábitat de nidificación por el Búho Real en un área mediterránea semiárida en la región de Murcia. Para ello se han cuantificado 14 variables que describen el grado de humanización, las características fisiográficas del roquedo, el paisaje vegetal, la competencia intraespecífica y la disponibilidad indirecta de alimento en torno a 23 roquedos con nidos y a 23 roquedos no ocupados por la especie. El Búho Real selecciona para nidificar roquedos de pequeñas dimensiones, en zonas de baja pendiente y poco accesibles. La presencia de conespecíficos se perfila como el principal factor limitante en la selección por el Búho Real del cortado de cría, hecho probablemente relacionado con una saturación de Búhos Reales en el área de estudio. Estos resultados contrastan con los obtenidos para esta especie en el norte de España.

Palabras clave: ambientes semiáridos, *Bubo bubo,* factores limitantes, nidificación, selección de hábitat, sureste de España.

SUMMARY.—*Nest-site selection by the Eagle Owl* Bubo bubo *in semi-arid Mediterranean habitats*. The factors presumably limiting Eagle Owl distribution in a semi-arid Mediterranean habitat (Murcia Region, southeastern Spain) were studied. Habitat features of 46 cliffs were characterized, incluiding cliffs with nests (n = 23) and cliffs where the species has never been detected (n = 23). For each cliff, 14 variables evaluating habitat humanisation, phisiography, vegetation, intraspecific competition and prey availability were quantified (Table 1). Eagle Owls selected smaller cliffs of lower accessibilty and located on less step slopes than those available (Table 2). This selection could be related to the optimization of the energetic costs of hunting. We observed negative relationships between cliff height and variables measuring habitat humanisation. In the semi-arid habitats considered here, the main limiting factor for Eagle Owl settlement seems to be the presence of conspecifics, a fact that is probably related to the high density of Eagle Owls (Table 2). Variables related to vegetation types, prey availability and habitat humanisation around cliffs did not differ between sites either occupied or unoccupied by Eagle Owls (Table 2). Our results differ from previous studies carried out in northern Spain, where Eagle Owl distribution seems to be limited by the availability of European rabbits *Oryctolagus cuniculus* as well as by human disturbance (Donázar, 1988).

Key words: *Bubo bubo,* limiting factors, nest-site selection, semi-arid habitats, southeastern Spain.

INTRODUCCIÓN

En España los estudios de selección de hábitat de cría de aves rapaces se han centrado tradicionalmente en especies de gran tamaño tales como el Quebrantahuesos *Gypaetus barbatus,* el Águila Imperial Ibérica *Aquila adalberti,* el Águila-azor Perdicera *Hieraaetus fasciatus* y el Alimoche Común *Neophron percnopterus* (Ceballos & Donázar, 1989; González *et al.*, 1992; Donázar *et al.*, 1993; Gil-Sánchez *et al.*, 1996; Ontiveros, 1999). En estos trabajos, la obtención de datos relativos al hábitat de nidificación se destaca como un elemento de gran importancia para la planificación de acciones de manejo y conservación de las poblaciones, dado que la humanización del medio y la alteración del hábitat, entre otros factores, pueden condicionar la selección del lugar de nidificación por estas aves (Newton, 1979; Mikkola, 1983).

El Búho Real *Bubo bubo* ha sido objeto de numerosos estudios en diferentes áreas del Paleártico Occidental (Mikkola, 1983; Cramp, 1985). Estos estudios se han dirigido fundamentalmente a recabar información sobre diferentes aspectos de sus hábitos alimenticios (Hiraldo *et al.,* 1976; Donázar, 1989; Korpimäki *et al*., 1990; Bayle, 1996) y de su biolo-

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gía reproductora (Bergier & Badan, 1979; Olsson, 1979; Wickl, 1979; Cugnasse, 1983; Donázar, 1990). No obstante, los requerimientos de hábitat del Búho Real son poco conocidos y las aproximaciones al estudio de éstos han sido de carácter cualitativo (Choussy, 1971; Blondel & Badan, 1976; Mysterud & Dunker, 1982), a excepción del trabajo realizado por Donázar (1988), en el cual se efectúa un análisis cuantitativo de la selección del hábitat de nidificación por esta especie en el norte de España. Hasta la fecha no se han abordado estudios encaminados a describir el patrón de selección de hábitat de cría de esta especie en hábitats mediterráneos semiáridos, donde el Búho Real es abundante y existe una alta disponibilidad de Conejo *Oryctolagus cuniculus* (Sánchez-Zapata, 1999), su presa básica y limitante de su distribución en latitudes más norteñas (Donázar, 1988).

El Búho Real es una especie común en la región de Murcia, que alberga una población estimada en torno a las 200-220 parejas con densidades de 1 pareja/54,4-62,1 km^2 (Sánchez-Zapata *et al*., 1995). Esta especie alcanza las mayores densidades en la mitad sur debido a la mayor abundancia de su principal presa, el conejo. Sus hábitos de nidificación son fundamentalmente rupícolas, aunque puede criar en el suelo y en los árboles. A escala de paisaje selecciona ambientes agrestes termófilos de baja y media altitud, dominados por una vegetación rica en matorrales y cultivos de secano y regadío (Sánchez-Zapata *et al*., 1995).

El objetivo de este trabajo es describir cuantitativamente la selección del hábitat de nidificación por el Búho Real en un área litoral de la región de Murcia, comparando hábitats ocupados y no ocupados de esta especie en relación con diferentes tipos de variables relacionadas con el grado de humanización, las características fisiográficas de los roquedos, el paisaje vegetal, la competencia intraespecífica y la disponibilidad de alimento.

ÁREA DE ESTUDIO Y MÉTODOS

El área de estudio, con una extensión de 1.300 km^2, se localiza en las sierras prelitorales y litorales de la región de Murcia, en el sureste de España. Se trata de una zona montañosa (0-888 m.s.n.m.) con un clima mediterráneo de tipo semiárido. Las precipitaciones no superan los 300 mm anuales y la vegetación natural está compuesta principalmente por matorrales adaptados a las condiciones de aridez, alternados con cultivos agrícolas de secano (almendro, olivo) y de regadío (especialmente invernaderos) y con bosques de pino carrasco *Pinus halepensis* de escasa extensión.

La localización de los territorios ocupados por el Búho Real fue realizada mediante censos nocturnos desde noviembre de 1986 hasta enero de 1987, utilizando reclamos sonoros (Fuller & Mosher, 1981). Los nidos fueron detectados mediante prospecciones a pie y observación con telescopio y prismáticos de 20 y 8 aumentos, respectivamente, de todos los lugares apropiados para la instalación del nido. La totalidad de los nidos analizados de este estudio se encuentra en roquedos, aunque a veces se han detectado puestas en simas de minas abandonadas o en el suelo (Sánchez-Zapata *et al*., 1996). La población estudiada representa el 13% de la población murciana estimada en 1991 (Sánchez-Zapata *et al*., 1995).

Para la caracterización del hábitat se ha procedido a comparar los territorios ocupados por la especie con otros donde está ausente. La elección de los roquedos no ocupados fue realizada mediante selección al azar, aunque *a priori* se excluyeron todas las zonas de hábitat rechazadas por la especie, como son las zonas agrícolas de regadío, invernaderos y polígonos industriales. Para ello se cuenta con 23 roquedos que albergaron nidos de Búho Real, correspondientes a 23 parejas, y con 23 roquedos no ocupados que presentan las condiciones mínimas (tamaño y disponibilidad de cornisas, huecos y/u oquedades) para que pudiera instalarse una pareja de Búhos Reales. Se escogió el criterio de un radio de 1 km alrededor del nido para cuantificar las variables seleccionadas en la caracterización de cada roquedo.

Se consideraron un total de 14 variables descriptoras del entorno del hábitat de nidificación del Búho Real (Tabla 1). Las variables 1-5 describen el grado de humanización, las variables 6-8 describen las características fisiográficas alrededor del nido, las variables 9-10 cuantifican la disponibilidad de alimento, la variable 11 estima la potencial competencia intraespecífica y las variables 12-14 estiman los tipos de vegetación y usos del suelo alrededor del lugar de nidificación. La información relativa a distan-

TABLA 1

Abreviaturas y descripción de las variables utilizadas en el estudio.
[Abbreviations and description of the environmental variables used to characterise cliffs either occupied or not occupied by Eagle Owls in southeastern Spain.]

Abreviatura *[Abbreviation]*	Definición *[Definition]*
DNH	Distancia en kilómetros al núcleo habitado permanente más próximo al nido. *[Distance (km) to the nearest urban centre.]*
DC	Distancia en kilómetros a la carretera más cercana al nido. *[Distance (km) to the nearest paved road.]*
DPF	Distancia lineal en kilómetros a la pista forestal más próxima al nido. *[Distance (km) to the nearest unpaved road.]*
NKC	Longitud en kilómetros de caminos y carreteras en un radio de 1 km alrededor del nido. *[Kilometres of tracks and paved roads in a 1 km circle around the nest site.]*
TMH	Tiempo necesario para llegar caminando al nido. Minutos empleados en llegar caminando desde el automóvil hasta el nido o punto más cercano a él. *[Estimate (min) of difficulty of access by foot up to the nest.]*
PEN	Pendiente media de la cuadrícula UTM de 1 x 1 km en que se encontraba el nido. *[Mean slope in the 1 x 1 km UTM square in which the nest was located.]*
ALT	Altitud en metros del roquedo sobre el nivel del mar. *[Altitude above sea level (m).]*
ALR	Altura en metros del roquedo. *[Cliff height (m).]*
BAS	Número de basureros permanentes alrededor del nido. *[Number of rubbish dumps in a 1 km circle around the nest site.]*
RAM	Longitud en kilómetros de rambla (cauce principal) alrededor del nido. *[Kilometres of wadi in a 1 km circle around the nest site.]*
VEC	Distancia al nido de Búho Real más cercano. *[Distance to the nearest-neighbor pair of Eagle Owls (km).]*
MAT	Superficie en hectáreas de matorral en un radio de 1 km. *[Surface (ha) covered by shrublands in a 1 km circle around the nest site.]*
CUL	Superficie en hectáreas de cultivos en un radio de 1 km. *[Surface (ha) covered by crops in the circular sampling area.]*
MAB	Superficie en hectáreas de matorral arbolado en un radio de 1 km. *[Surface (ha) covered by shrublands with trees in a 1 km circle around the nest site.]*

cias, longitudes de vías de comunicación y pendientes, así como los usos del suelo, ha sido extraída de la cartografía 1:25.000 del Instituto Geográfico Nacional.

La estima de la abundancia de presas se realizó de modo indirecto. En el área de estudio, el conejo, las ratas *Rattus* spp., la Perdiz Roja *Alectoris rufa* y los colúmbidos *Columba* spp. son las presas más habituales en la dieta del Búho Real (Martínez *et al*., 1992). La presencia de basureros alrededor de los nidos fomenta la aparición de ratas, en especial de rata parda *Rattus norvegicus*, pudiendo provocar una fuerte preferencia por esta presa dada su alta disponibilidad en este tipo de ambientes (Willgohs, 1974; Donázar, 1988). El Búho Real es el ave de presa europea más especializada en la captura de conejos (Delibes & Hiraldo, 1981). Este mamífero construye habitualmente sus madrigueras en terrenos blandos de hábitats abiertos con presencia de cobertura vegetal (Rogers *et al*., 1994). En este sentido la disponibilidad de ramblas, con la consiguiente oferta de sustratos blandos en las proximidades de los nidos de la estrigiforme, pudiera reflejar la disponibilidad de esta presa en los ambientes mediterráneos áridos y semiáridos.

Las posibles diferencias en las variables han sido examinadas mediante la prueba no paramétrica de Kruskall-Wallis (Sokal & Rohlf, 1997). En el análisis de datos no hemos aplicado la corrección secuencial de Bonferroni dado que consideramos que las medidas de cada una de las variables son independientes (véase Cabin & Mitchell, 2000). Asimismo, aplicamos correlaciones de Spearman para examinar las posibles relaciones entre las variables analizadas.

RESULTADOS Y DISCUSIÓN

En la Tabla 2 se recogen los valores de media y desviación típica de las variables medidas en torno a los roquedos ocupados por el Búho Real y los escogidos al azar. Se obtuvieron diferencias significativas para cuatro variables: accesibilidad, altura del roquedo, pendiente y distancia a la pareja de Búho Real más próxima.

Nuestros resultados muestran que el Búho Real selecciona roquedos de pequeñas dimensiones, en zonas de baja pendiente y poco accesibles. La preferencia del Búho Real de cortados pequeños frente a grandes resulta *a priori* un tanto sorprendente. Varios autores han señalado la preferencia del Búho Real y del Águila-azor Perdicera hacia los roquedos de mayores dimensiones en zonas abruptas, especialmente en ambientes humanizados (Donázar, 1988; Ontiveros, 1999; Sánchez-Zapata, 1999). La selección por el Búho Real de pequeños cortados puede estar relacionada con optimizar los costes energéticos de la actividad de caza. Los traslados de presas a nidos situados en cortados elevados pueden resultar energéticamente limitantes para la especie debido a su considerable carga alar (0,71 gr/cm^2; Brull en Mikkola, 1983) y a la ausencia de corrientes térmicas durante la noche (Donázar, 1988). No obstante, podría ocurrir que en el área de estudio los cortados escogidos por el Búho Real fueran los de menor tamaño por estar alejados de zonas humanizadas. No hemos encontrado correlaciones significativas entre la altura del roquedo y las variables de humanización (DNH: r_s = –0,125, P > 0,05; DC: r_s = –0,183, P > 0,05; DPF: r_s = –0,002, P > 0,05; NKC: r_s = 0,027, P > 0,05), lo cual descartaría esta hipótesis alternativa.

TABLA 2

Características de los roquedos analizados (media y desviación típica) y resultados de las pruebas de Kruskall-Wallis (*H*) entre los roquedos con presencia de Búho Real y los roquedos no ocupados.
*[Habitat features (mean and standard desviation) of the cliffs either occupied or not occupied by Eagle Owls in southeastern Spain. Results of Kruskall-Wallis tests (*H*) for differences in these habitat features are also shown.]*

	Ocupados (*n* = 23) *[Occupied]*	Azar (*n* = 23) *[Unoccupied]*	H	*P*
DNH	2,03 (0,93)	1,94 (0,71)	0,0011	0,9737
DC	1,60 (0,82)	1,19 (0,72)	2,2996	0,1294
DPF	0,51 (0,28)	0,43 (0,20)	1,0681	0,3014
NKC	0,80 (0,75)	0,92 (0,60)	1,0998	0,2943
TMH	24,26 (11,01)	10,80 (9,84)	12,7669	0,0004
PEN	6,60 (3,00)	9,05 (3,70)	5,6306	0,0176
ALT	377,83 (141,60)	382,90 (190,60)	0,0121	0,9124
ALR	14,30 (11,03)	23,30 (12,91)	8,2075	0,0042
BAS	0,48 (0,73)	0,35 (0,57)	0,2300	0,6315
RAM	0,70 (0,54)	0,52 (0,36)	0,6016	0,4380
VEC	3,77 (3,13)	2,27 (1,83)	4,5009	0,0339
MAT	237,12 (66,16)	224,30 (72,20)	0,2571	0,6121
CUL	24,72 (26,32)	51,50 (53,40)	3,5005	0,0613
MAB	37,01 (63,50)	19,40 (33,70)	0,6812	0,4092

Los roquedos ocupados por el Búho Real son poco accesibles a las personas. Este hecho pudiera ser reflejo de la sensibilidad de la especie a la persecución directa, uno de los factores más importantes en la mortalidad no natural del Búho Real en la zona de estudio y otras áreas del Paleártico (Mikkola, 1983; Hernández, 1989; Martínez *et al*., 1992; Tucker & Heath, 1994).

La distancia entre el roquedo ocupado y la pareja de Búho Real más próxima es significativamente mayor que la media disponible. Este resultado parece indicar que la selección del roquedo de cría por el Búho Real responde a la presencia de conespecíficos. Esto pudiera ser debido a que el área de estudio, rica en presas, se encuentra próxima a la saturación por Búhos Reales. Esta situación es contraria a la observada en el norte de España, en una zona pobre en presas y con baja densidad de Búhos Reales, donde la influencia de la variable distancia al vecino más próximo actuaba en sentido contrario, presumiblemente debido a una distribución contagiosa de las aves en enclaves adecuados (Donázar, 1988).

La vegetación circundante al nido no parece tener ninguna influencia en la ubicación de éste. Aunque nuestros datos apuntan a que los roquedos ocupados por el Búho Real presentan una vegetación más conservada (menor superficie de cultivos de secano y mayor superficie de matorral arbolado) en su entorno, las diferencias no fueron significativas. Esta débil relación entre el paisaje vegetal y las zonas de cría de la especie coincide con la expuesta para ésta y otras rapaces en diferentes áreas mediterráneas (Parellada *et al*., 1984; Donázar *et al*., 1989; González *et al*., 1992).

En el área mediterránea, los roquedos preferidos por el Búho Real se encuentran a baja altitud debido a que se localizan en las zonas de hábitat idóneas para el conejo (Blondel & Badan, 1976; Donázar *et al*., 1989). Sin embargo, en este estudio no hemos encontrado relaciones positivas entre la presencia del Búho Real y la oferta de alimento (ratas y conejo), quizás debido al empleo de estimadores indirectos de su disponibilidad.

En síntesis, los resultados obtenidos en el presente estudio muestran que los factores limitantes del hábitat de cría por el Búho Real en ambiente semiáridos son notablemente diferentes a los atribuidos para esta especie en el norte de España (Donázar, 1988).

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Habitat selection in *Psammodromus algirus* (LINNAEUS, 1758) (*Sauria*: *Lacertidae*): age related differences

Dobór środowiska u *Psammodromus algirus* (LINNAEUS, 1758) (*Sauria*: *Lacertidae*): różnice związane z wiekiem

Abstract. Habitat selection in adult and juvenile *Psammodromus algirus* was studied along a Mediterranean successional gradient in southwestern Iberia. Both age classes showed patterns of habitat selection which differed significantly from a random survey of the habitat. These patterns were different in the two age classes. Juveniles occupied less wooded microhabitats with a denser low vegetation. Some morphological parameters thought to be related to habitat-use were measured; these did not differ between adults and juveniles. The biological meaning of the observed differences is discussed: intraspecific hostile interactions and predator avoidance are though to be involved, rather than thermal requirements.

I. INTRODUCTION

Several studies of age dependant variation in habitat selection have been made in lizards, including the families *Iguanidae* (COLLETTE 1961; SCHOENER 1967; JENSSEN 1970; DAVIES and VERBEEK 1972; RUIBAL and PHILIBOSIAN 1974; MOERMOND 1979; FOX 1983; STAMPS 1983a and 1983b), *Teiidae* (SCHALL 1974) and *Agamidae* (BRADSHAW 1971). The observed differences among various populations segments were attributed to morphology-determined differences in the required structure of the environment (MOERMOND 1979), different thermal requirements (STAMPS 1983a and 1987), vulnerability to predation (STAMPS 1983b) or intraspecific competition (BRADSHAW 1971; SCHALL 1974; FOX 1983).

The aim of this paper is to analyze the habitat selection and spacing patterns of a Mediterranean species of *Lacertidae*, a family which has received little attention in this sense (see STAMPS 1977 for a review). The animal of choice is *Psammodromus algirus* (LINNAEUS, 1758), a fairly abundant but little known lizard (though see MELLADO 1980 and review by BÖHME 1981) inhabiting the Mediterranean shrublands and forests of the Iberian Peninsula. We consider whether if there are differences in habitat selection between juvenile and adult *P. algirus*, and we examine the ecomorphological, thermoregulation and social interaction hypotheses in order to suggest an explanation for the observed pattern of habitat choice.

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II. MATERIAL AND METHODS

Habitat selection was studied along a habitat gradient in the coast of Cádiz, southwestern Spain (Chiclana de la Frontera, 30°26'N 00°09'W). The gradient consisted of a well defined series of forest succession stages including a cleared pine forest of *Pinus pinea* and *Quercus suber*, a Mediterranean shrubland of *Cistus* spp. and *Halimium* spp., a xerophyte grassland and a sand dune area with bushes of *Juniperus phoenicia*. For a more detailed description of the physical structure of the study area, see the values of R (random survey) in Table I.

Table I

Substrate and plant cover percentages (mean and standard deviation) for juvenile and adult *Psammodromus algirus* vs random (R) survey of the habitat

	Juveniles		Adults		R	
Variables	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
CS Cover of sand	31.7	29.7	35.1	35.9	50.2	40.2
CL Cover of litter	74.3	27.1	69.1	35.2	46.7	37.4
CO Plant cover at the ground level	55.9	28.8	46.4	27.3	34.7	27.4
C5 Plant cover at 5 cm above the ground	60.2	21.2	56.0	25.1	52.0	29.4
C10 Plant cover at 10 cm above the ground	49.1	20.2	45.2	23.5	42.0	26.0
C30 Plant cover at 30 cm above the ground	23.3	17.4	23.2	17.6	22.6	17.7
C50 Plant cover at 50 cm above the ground	12.2	12.0	11.9	12.4	11.5	12.2
C70 Plant cover at 70 cm above the ground	6.5	8.4	6.1	7.8	5.5	7.8
CT Cover of trees	20.9	30.0	25.7	30.5	12.6	25.8
CH Cover of herbs	67.8	24.8	58.8	26.0	53.6	30.5
CJ Cover of *Juniperus phoenicia*	1.7	6.9	4.1	12.2	3.3	8.6
CB Cover of bushes (*Cistus and Halimium*)	43.3	25.3	36.9	23.7	32.8	32.5
Number of samples	(27)		(44)		(113)	

Sampling was performed by walking in a randomly chosen direction for seven hours each morning and afternoon in April 1985. Since in this species hatching takes place in late summer and early autumn (Salvador 1985), each lizard observed was assigned to one of the two following age-classes: juveniles (those born in the last breeding season) and individuals older than one year.

When a lizard was first observed, two orthogonal ten metres transects were examined, intersecting at the point of initial sighting. The presence of the habitat attributes listed in Table I was noted, with a stick scored at different heights, at 1m-intervals. This survey method provided an overall picture of habitat structure, composed of 20 sample points per lizard observation, that allowed the calculation of substrate and plant cover percentages. The same sampling design was employed at 113 randomly chosen spots that were used for comparison between availability and actual utilization of spatial resources. This sampling method is similar to the point-centered method used in studies of bird habitat selection (see for instance James and Shugart 1970; Noon 1981; and Ratti et al. 1984) and to those employed by Reagan (1974), and Scheibe (1987) with different reptilian taxa.

Morphological data were obtained from alcohol-preserved specimens deposited at the Museum of Vertebrate Zoology of the School of Biological Sciences at the Universidad Complutense of Madrid. The variables considered were snout-vent length, tibia length and tail length (the later was only measured on animals with unregenerated tails). Since the measurements of the limbs could not be taken from the bones, we adopted the criteria followed by Moermond (1979) in his ecomorphological analysis of *Anolis* lizard communities. To avoid body size effects, biometrical variables were standardized by considering their relative proportions (see Moermond 1979 for a similar approach and James and McCulloch 1985 for a general discussion).

In the statistical handling of data the t-test for means was used; though we did not find habitat-use differences between adults and juveniles, this result is interpreted as a consequence of the scarce sensibility of this test in the analysis of intraspecific differences, since population segments of a single species are expected to have similar basic ecological requirements. In addition, and despite the reasonably high available sample sizes ($n = 27$ for juveniles and $n = 44$ for adults), the high variance values produce an undesirable increase in the magnitude of type II error. Therefore, we have employed a different statistical design based on the comparison of both age classes with the series of data obtained by random sampling ($n = 113$), which can be regarded as an „ecological constant" (habitat availability) with a very low standard error. This design thereby evaluates habitat selection (use vs availability) in juveniles and adults.

III. RESULTS

T-test comparisons between mean cover values of both adults and juveniles vs random sampling (Table I) were used to identify the main trends in habitat selection. Table II shows that the species as a whole selects its position along the habitat gradient: nine out the 24 t-test performed reflect differences between availability and actual utilization of habitat variables at a significance level of 0.05, a number which is significantly higher (G-test, $p < 0.001$) than the one expected at random ($5 \times 24/100 = 1.2$).

Adult and juvenile lizards share a strong positive selection for microhabitats with a high percentage of litter cover and plant cover at the ground level (see table II). Aside from these features, there are marked differences (sometimes with one of the t-test results being non-significant and the other significant at $p < 0.01$) between the within-habitat distribution patterns of adults and juveniles. The latter differs from the former in not showing a strong selection for wooded areas and in positively selecting areas with high plant cover five and ten cm above the ground, high cover of herbs and high cover of *Cistus* and *Halimium* shrubs (Table II). Since there are no significant differences between the variances of both age-classes associated with tree cover (F-test, $p > 0.1$), it can be stated that juvenile *P. algirus* suffer a shift towards unwooded areas without increasing their spatial niche breadth. Juveniles therefore occupy relatively less wooded microhabitats with a denser vegetation of herbs and shrubs five and ten cm above the ground.

Table II

T-test comparison between mean percentages of available substrate and plant cover (random sampling) and actual patterns of habitat-use by juvenile and adult *P. algirus*; symbols of variables as in Table I. +: p 0.05; ++: p 0.01; +++: p 0.001

	CS	CL	CO	C5	C10	C30	C50	C70	CT	CH	CJ	CB
Juveniles	ns	+++	+++	+	+	ns	ns	ns	ns	++	ns	+
Adults	ns	+++	++	ns	ns	ns	ns	ns	++	ns	ns	ns

Although little is known about allometry in lacertids, it would be reasonable to suspect that anatomical structures related to locomotion (e.g., limbs or limb segments) could change their relative proportions during growth, thus enabling their owners to undergo a spatial segregation of age classes that would facilitate intraspecific resource partitioning. Nevertheless, from the results of t-tests comparisons shown in Table III it is made clear that there are no significant differences between adults and juveniles in any of the morphological parameters considered (i.e. hind leg length relative to snout-vent length, tibia relative to femur, humerus relative to femur and tail relative to snout-vent length; see Moermond 1979 for an ecomorphological interpretation of these ratios). It can therefore be concluded that the functional relationship between morphology and habitat-use does not determine the observed shift of juvenile lizards towards areas with lower, more open vegetation.

Table III

Morphological comparison of juvenile and adult *P. algirus* (morphological ratios modified from Moermond 1979)

	Juveniles			Adults			t-tests
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	p
Hindleg: snout-vent	0.32	0.021	15	0.32	0.019	15	0.99
Tibia: femur	0.86	0.060	15	0.84	0.057	15	0.20
Humerus: femur	0.76	0.047	15	0.74	0.051	15	0.20
Tail: snout-vent	2.38	0.171	12	2.40	0.229	13	0.50

IV. DISCUSSION

Previous research (see Heatwole 1977 for a review) has identified at least two potentially important factors for habitat-selection in reptiles: physical structure of the environment and microclimate. Habitat structure is relevant because, given a particular morphology, the geometric arrangement of the environment determines its suitability for foraging and locomotion (Pianka and Pianka 1976; Pianka 1979; Moermond 1979). Nevertheless our results indicate a complete lack of ontogenetic change in morphology between juvenile and adult lizards, thus leaving unexplained the observed shift in habitat selection with age.

Similarly, homesite selection by juvenile *P. algirus* is apparently not related to the thermal environment, since thermoregulatory patterns seem to be fairly constant over a wide range of body sizes. Thus, circadian activity rhythms of juvenile and adult *P. algirus* are indistinguishable on a round year basis in a Mediterranean holm-oak wood (Cano 1984), and neither the basking frequency nor the relationship between the body and ambient temperatures show statistical differences associated with age or body size (Diaz 1988).

An alternative explanation of the observed distribution pattern is that microhabitat differences could be the result of social interactions, with dominant adult lizards excluding juveniles from optimal quality homesites. According to the model of lizard spacing pattern postulated by Stamps (1977), such dominance relationships are expected to occur among lacertid species under conditions of poor visibility (a characteristic of Mediterranean forests and shrublands) and local clumping (caused by the tendency of *P. algirus* to concentrate around the vegetation patches). The aggressiveness of adult lizards towards their smaller conspecifics is furtherly proved by the fact that they occasionally eat juveniles of their own species (Mellado 1980). In addition, we have observed fleeing reactions in experimental enclosures, smaller males (subordinates) being displaced by larger ones (dominants) in almost every case. If we accept the influence of social hierarchies on the within-habitat distribution of the species, then the differences in body weight must be essential in determining the outcome of hostile interactions (Wallace 1987) and hence the distribution patterns of both population segments.

The available data (Valverde 1967) indicate that *P. algirus* is an important prey item for many visually-guided predators in Mediterranean food chains, suggesting that a displacement towards open areas would be associated with higher predation risks. *Falco tinnunculus* and *Lanius excubitor* were present in the study area, as well as other possible predators mentioned by Valverde (1967). Escape speed is lower in juveniles due to their smaller body size (pers. obs.; see Stamps 1983a; and Avery et al. 1987). This would imply that the occupation of denser vegetated areas at the ground level (see Results and Table II) could reflect a search for predator-refuges where juveniles would be less detectable (see Stamps 1983b for a related experiment with *Anolis aeneus*).

The foregoing arguments suggest that agonistic interactions seem to be involved in the observed habitat shift between juvenile and adult *P. algirus*, rather than ontogenetic differences in habitat selection patterns (see Heatwole 1977 for a similar conclusion).

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