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Habitat Selection and Habitat Suitability Preferences

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Why Select or Prefer a Given Habitat?
Which Habitats and Which Constraints for Different Choices?
How Select a Habitat?

Individual and Population Implications of Habitat Selection
Further Reading

Why Select or Prefer a Given Habitat?

Definition of Habitat and Habitat Patch

For most species, the environment is heterogeneous at various spatial and temporal scales (**Figure 1**). A habitat can be defined by a given type of environment characterized by general physical features (e.g., type of vegetation, water, or soil structures). The habitat of a species can also be defined by the general characteristics of the areas used by individuals, which must be suitable enough for the species' activities. This definition results from the observed spatial distribution of individuals. Finally, at a finer scale, a habitat can also be defined by the portion of the environment devoted to a particular activity of individuals (e.g., breeding or foraging). Usually, the term 'habitat' does not encompass conspecifics, that is, the social components of individuals' activities, contrary to the term 'environment'. A habitat patch can be defined as a continuous and homogeneous portion of a habitat (**Figure 1**).

Definition of Habitat or Patch Suitability and Quality

A habitat is suitable for a species when it contains all resources needed for a given activity in sufficient quantity (e.g., food when foraging, nest sites when breeding). Individuals can only live in suitable habitats; thus by definition, habitats where individuals are found to live or perform a given activity must be suitable. Habitat suitability can be difficult to define using other criteria
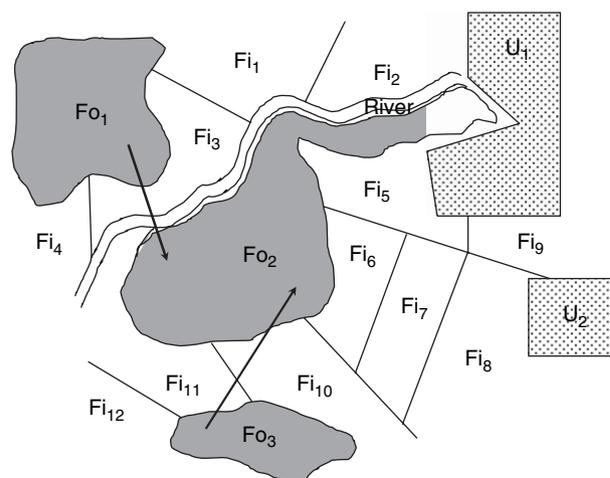
Figure 1 An illustration of environmental spatial heterogeneity defining habitats and habitat patches. In this schematic farmland landscape, portions of the environment are constituted by a river, fields (delimited by straight lines), forests (gray zones), and urban areas (dashed zones), which have very different general physical characteristics and define four different habitats. Within each habitat type, several continuous and homogeneous subareas can be found and define habitat patches: Fo_1 to Fo_3 (forest), Fi_1 to Fi_{12} (fields), U_1 and U_2 (urban areas). Patches of the same habitat can vary in quality; for instance, different types of crops may generate different amounts of food or breeding sites availability in different fields.

than the observed repeated and long-term presence of individuals.

Suitable habitats and patches for a given species can differ by some intrinsic characteristics affecting individuals' fitness (e.g., available resource quantity and quality,

level of competition for resources or predation). The quality of a habitat or patch is usually defined by the fitness (measured, e.g., by energy gains per time unit or reproductive output) that can be achieved by individuals in this habitat or patch: a habitat or patch in which individuals achieve high fitness is defined as a high-quality habitat or patch, relative to other habitats and patches. Within the framework of foraging and breeding habitat choice, the quality of habitats is usually evaluated in terms of energy intake rate and reproductive success, respectively.

Spatiotemporal Variability of Habitat Suitability and Quality Leads to Habitat Selection

In heterogeneous environments, natural selection will favor individuals capable of occupying the most favorable areas for activities linked to fitness, that is, survival and reproduction. Spatial and temporal environmental heterogeneity (**Figure 2**) thus leads to selective pressures favoring behaviors that allow individuals to select high-quality habitats or patches, that is, the evolution of individual strategies of habitat choice, for any activity considered (e.g., foraging for food, searching for a sexual partner, finding shelter from predators, breeding).

Spatial heterogeneity and temporal predictability of habitat or patch quality are required conditions for habitat choice or preference to evolve (**Figure 2**). In a homogeneous and equally exploited environment, there is no need for individuals to choose because the expected fitness will be equal in all habitats or patches. Moreover, if the environment is not predictable at the relevant timescale for the activity considered, a location cannot be chosen based on given characteristics since they could randomly change in the time between gathering information on those characteristics and individual decision, thus preventing individuals to achieve the expected fitness.

Habitat choice can have a major impact on fitness. Wrong decisions can lead to highly reduced survival, or complete breeding failure. Habitat or patch choice will be all the more critical as the temporal scale involved is long and individuals' movements are spatially constrained, for example, breeding compared to foraging habitat selection. The habitat used for breeding also determines the conditions to which breeders will be exposed during this period of life, sometimes representing most of an individual's lifetime. Selective pressures on habitat choice are thus strong.

Sources of Variation in Habitat Suitability and Quality

Spatial and temporal heterogeneity in habitat or patch suitability and quality can be due to many different factors linked to abiotic, biotic, and social characteristics.

The physical characteristics of the environment that can affect fitness vary from climatic conditions (rain, wind, and temperature regimes), soil nature (e.g., for species that dig burrows), stability of the substratum (e.g., when breeding on a slope or in a tree), level of salinity (for marine species), etc., depending on the species considered. Biotic sources of environmental variation include the availability of biotic resources (e.g., food and nest-building materials), which may be required in sufficient quantity as well as quality (e.g., required nutrients may only be available in specific food items); predators and parasites are often spatially heterogeneous biotic factors.

Finally, social components can play a major role. The density of conspecifics or heterospecifics exploiting the same resources can vary drastically in time and space, and competitors' presence may reduce the fitness of a given individual directly (e.g., when resources are limited) or indirectly (e.g., via the attraction of common predators). Because conspecifics also have to select and secure resources, their distribution among habitats and patches will affect the relative quality of potentially available resources. Conspecific decisions affect fitness gains expected by individuals choosing a particular habitat or patch (i.e., a frequency-dependent process). Conversely, conspecifics' or heterospecifics' presence can also have positive fitness effects, for example, when individuals interact with each other to capture preys, deter predators, build nests, etc., so that when conspecific density decreases below a certain value, individuals' fitness decreases (Allee effect). Conspecifics' presence can also be beneficial by providing information about habitat or patch quality. Both conspecifics' quantity and quality may vary and thus affect breeding habitat quality. In particular, the relatedness between individuals can affect local habitat quality, through kin competition or cooperation.

In many cases, individuals will require several different critical resources simultaneously. All the fundamental ecological requirements for a given activity thus have to be accounted for. For instance, a breeding patch may provide large amounts of food, but lack breeding sites, and thus will not be used. The different factors affecting fitness are also likely to interact with each other. Furthermore, spatiotemporal variations of important factors likely show different patterns at different scales, generating tradeoffs between factors, since the values of the different factors that maximize individual fitness may not occur in the same locations at the same time. These tradeoffs may themselves differ in time and space.

Scales of Variation in Habitat Suitability and Quality

The importance of a given factor for habitat choice varies with its spatiotemporal variability. Local habitat quality can vary at different scales, both spatially (e.g., between
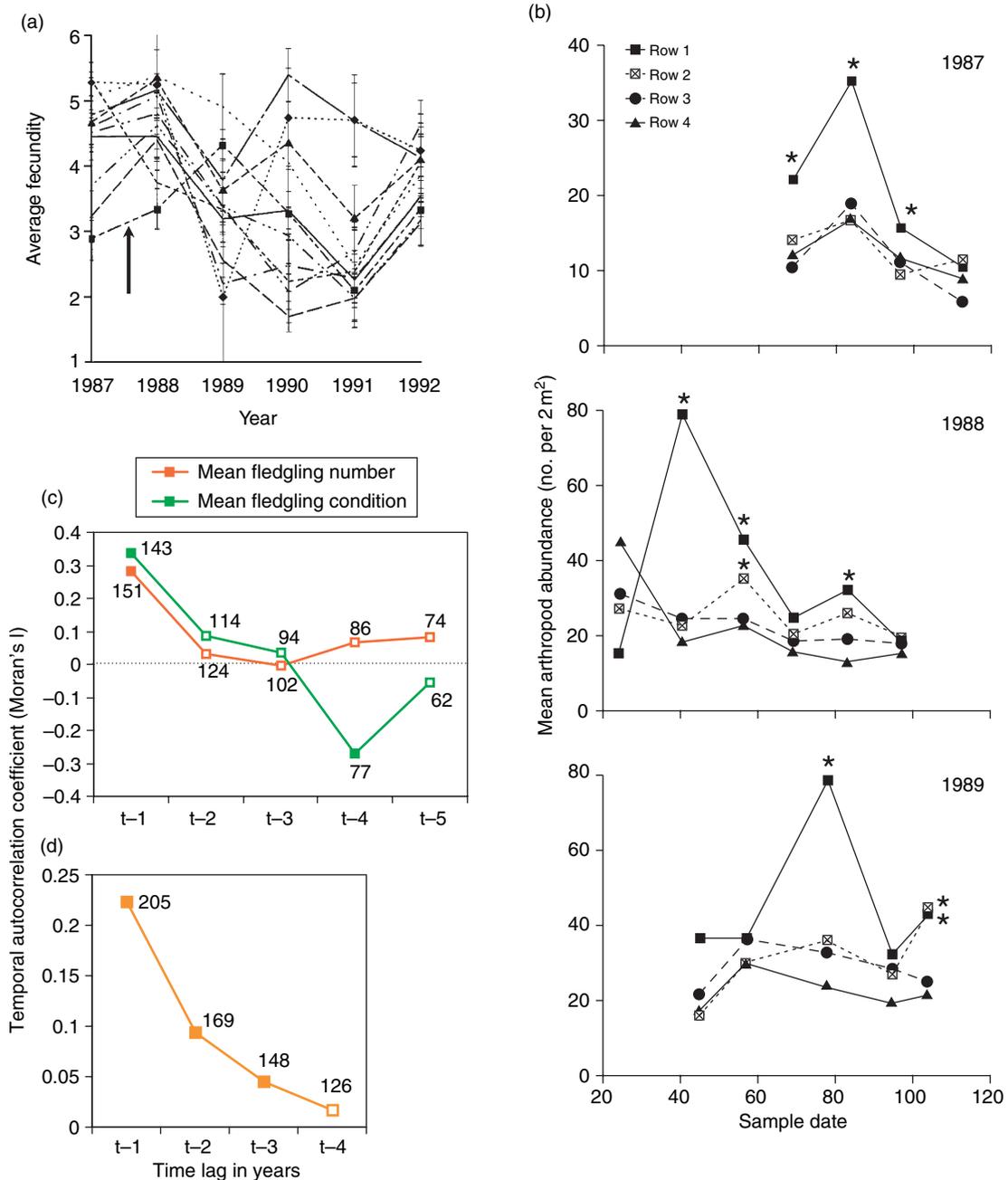
Figure 2 Illustration of the spatiotemporal variation of habitat quality from several field studies. (a) Mean fecundity (number of young fledged per reproductive event ± 1 SE) of collared flycatchers (*Ficedula albicollis*) in a series of 11 forest patches over 6 years. The relative quality of a patch differs between years: for example, the patch indicated by an arrow has the lowest mean fecundity in the first year, but the second highest fecundity 2 years later. (b) Mean prey abundance per 2 m^2 leaf surface in a flooded vegetation along shores that constitutes breeding habitat of prothonotary warblers (*Protonotaria citrea*) over 3 years, according to the localization of breeding site within patch. Sites are located in rows parallel to shoreline, with row 1 closest to, and row 4 farthest from, the shore (stars indicate significant differences). (c) Temporal autocorrelation of mean fledgling number and condition as measures of patch quality in collared flycatchers in a series of 20 forest patches over 20 years (closed symbols: significant coefficients). The autocorrelation fades after a time lag of 1 year. (d) Conversely, the temporal autocorrelation of patch reproductive success (mean number of fledged young per nest) for black-legged kittiwakes (*Rissa tridactyla*) stays significant for 3 years. (a) From Doncaster CPD, Clobert J, Doligez B, Gustafsson L, and Danchin E (1997) Balanced dispersal between spatially varying local populations: An alternative to the source–sink model. *American Naturalist* 150: 425–445. (b) Reproduced from Petit LJ and Petit DR (1996) Factors governing habitat selection by prothonotary warblers: Field tests of the Fretwell–Lucas models. *Ecological Monographs* 66: 367–387, with permission. (c) Data from Doligez B, Pärt T, Danchin E, Clobert J, and Gustafsson L (2004) Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* 73: 75–87. (d) Data from Danchin E, Boulinier T, and Massot M (1998) Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* 79: 2415–2428.

and within habitat patches) and temporally (**Figure 2**). Detecting spatial heterogeneity and temporal predictability is tightly linked with the scale considered. The environment may be homogeneous at a given spatial or temporal scale (e.g., within patches or hours), but heterogeneous at another scale (e.g., among patches or years). Habitat selection can involve a cascade of nested scales: individuals can first choose among habitat types, then a general area within a habitat type, and then within this area, a patch that may comprise several sites. The relevant spatial and temporal scales at which habitat choice needs to be investigated thus have to be identified. These scales are constrained by habitat heterogeneity itself, but also by the ability of individuals to detect heterogeneity. Individuals may choose between habitats only if they are aware of habitat or patch quality variation. The scales at which an individual perceives spatial heterogeneity (depending, e.g., on its movement ability) constrain habitat selection and define the upper scales of possible habitat choice. Only environmental factors affecting fitness and varying in time and space at the scales individuals can explore are therefore relevant to habitat choice.

Definition of Selection/Choice/Preference

Because of environmental heterogeneity, individuals face alternatives with different fitness outcomes. When confronted with multiple alternative situations, individuals eventually select one of them, and are said to perform a choice or prefer one option when the probability to choose this option is significantly higher than expected by chance, and is affected by the variation in the expected fitness among potential alternatives. In the classic expression 'habitat selection' (synonym of 'habitat choice'), the term 'selection' describes a process of individual choice using some decision rule (despite implying no conscious mechanism), which includes the processes of information acquisition about the quality of alternative habitats or patches, and information use to select the alternative expected to maximize fitness.

Because of competition, all individuals may however not be able to settle in the highest-quality, preferred habitat or patch, that is, the realized choice may not reflect individual's preference. This may be because individuals are prevented from choosing a habitat or patch by dominant competitors despite attempting to do so, or because individuals evaluate competition intensity beforehand and choose not to use these best habitats or patches. Furthermore, individuals may use different strategies than optimal habitat or patch choice, that is, choose a suboptimal patch but compensate for the decrease in

fitness using other strategies. For instance, individuals may choose to exploit different food sources, or adopt strategies limiting risks, rather than changing patch.

Which Habitats and Which Constraints for Different Choices?

Foraging Habitat Selection

The issue of finding and exploiting food is crucial. In heterogeneous environments, foraging habitat patches differ in quality depending on the availability of food resources and their intrinsic quality (e.g., nutritive value), but also on the costs associated to exploit these resources, involving access to food items in terms of energy, time, and injury risk when competing, risk of being preyed upon, of getting scrounged by con- or heterospecific competitors, etc. Spatial and temporal scales involved in foraging habitat selection can vary (e.g., from a few seconds up to days in large predators), but in most species, foraging habitat choices are made by individuals a large number of times over their entire lives. Decisions linked with foraging habitat selection include the choice of patches where to start foraging and duration of patch exploitation following progressive resource depletion over time, thus decision to depart to another foraging patch (**Figure 3**).

Theoretical models have been built and tested empirically to investigate which conditions affect these two types of decisions. Classical optimal foraging theory addresses the patch-time allocation that maximizes an individual's fitness by referring to the marginal value theorem (**Figure 4**), which states that the optimal strategy is to leave a foraging patch when the instantaneous fitness gain rate from the current patch falls below the average gain rate that can be achieved in the environment. The model predicts that individuals will stay longer (1) in a more profitable patch, (2) as the distance between patches (and thus travel time) increases, and (3) when the environment as a whole is less profitable (**Figure 4**). The marginal value theorem has been a useful tool but has however been criticized on the grounds that it makes simplified assumptions, in particular that foragers are optimal and have a complete knowledge of resource abundance and distribution in the environment, which is unrealistic. Linking the optimality predictions of the model with proximate mechanisms of patch departure decisions involved is necessary. Simple mechanistic rules for patch-leaving decisions have therefore been proposed and tested experimentally (**Figure 5**):

(a) *Incremental rule.* The probability to stay in the current patch decreases with unsuccessful search time spent in the patch, but increases each time a resource is found; individuals will find more resources items, and thus stay longer, in rich patches.

(b) *Decremental rule.* The probability to stay decreases each time a resource is found; individuals will thus stay shorter in high-quality patches.

(c) *Giving-up-time rule.* The tendency to stay decreases with unsuccessful search time spent on the patch, but each time a resource item is found, the tendency to stay is reset to a maximum level; individuals leave after a fixed unsuccessful search time (giving-up time).

(d) *Fixed-number rule.* The individual leaves the patch after a given, fixed number of resource items have been found.

(e) *Fixed-time rule.* The individual forages for a fixed period of time in each patch and leaves the patch independently of the number of resource items found.

Which decision rule will be adaptive depends on (1) the spatial distribution of resource items in the environment, which conditions the information about patch quality that
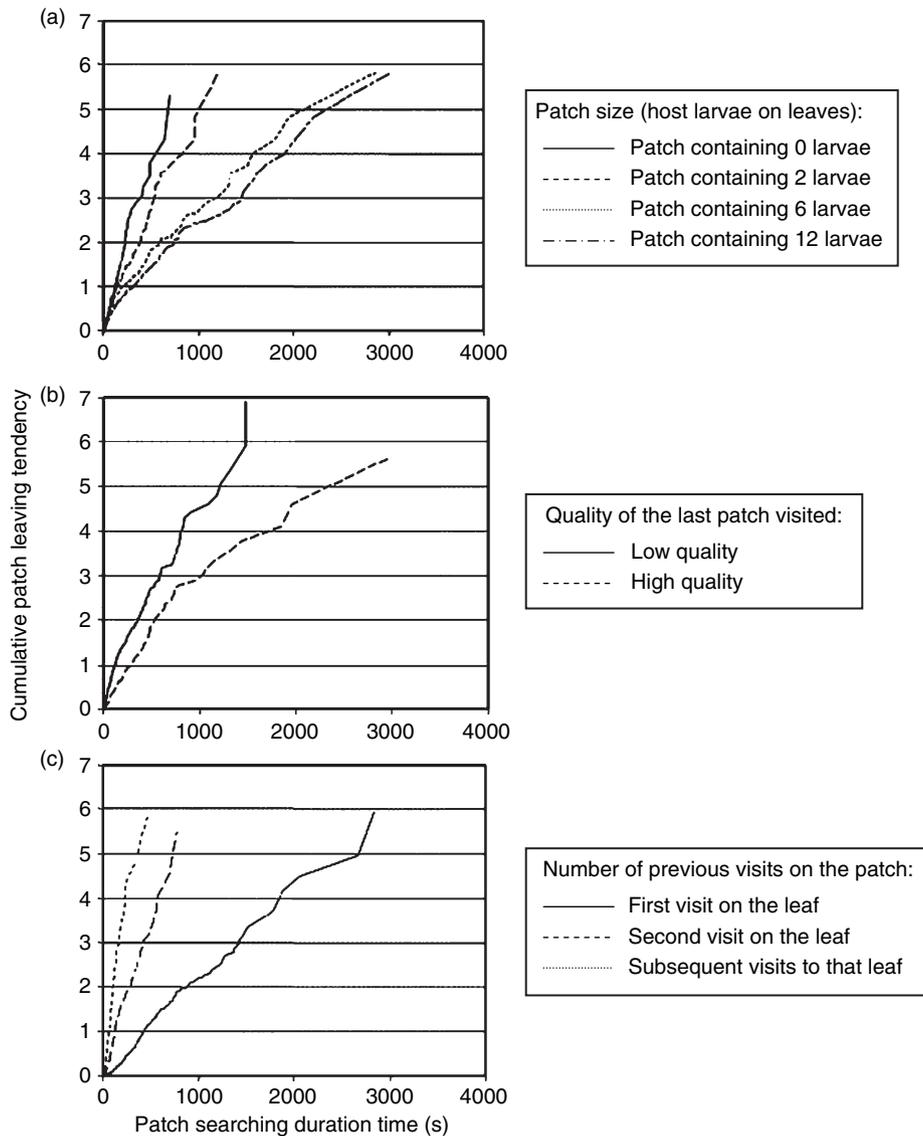

Figure 3 Foraging decisions in an insect parasitoid, *Aphidius rhopalosiphi*. Females of this parasitic wasp lay eggs in grain aphids *Sitobion avenae*, which are spatially distributed in discrete patches. Parasitic wasps have to adjust their searching time within a given host patch and allocate their foraging time among the different patches available in the habitat, to maximize their fitness. These decisions have to be based upon information on patch quality, obtained through both host encounter rate in the patch and previous searching experience by the wasp on the same or other patches. Patch-leaving decisions in this species depend on (a) host patch size, (b) quality of the last patch visited, and (c) previous experience in the current patch. Females spent more time in a patch when it contains more resources, when they just visited a high-quality patch, and during their first visit in the patch. From Outreman Y, Le Ralec A, Wajnberg E, and Pierre J-S (2005) Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behavioral Ecology and Sociobiology* 58: 208–217.
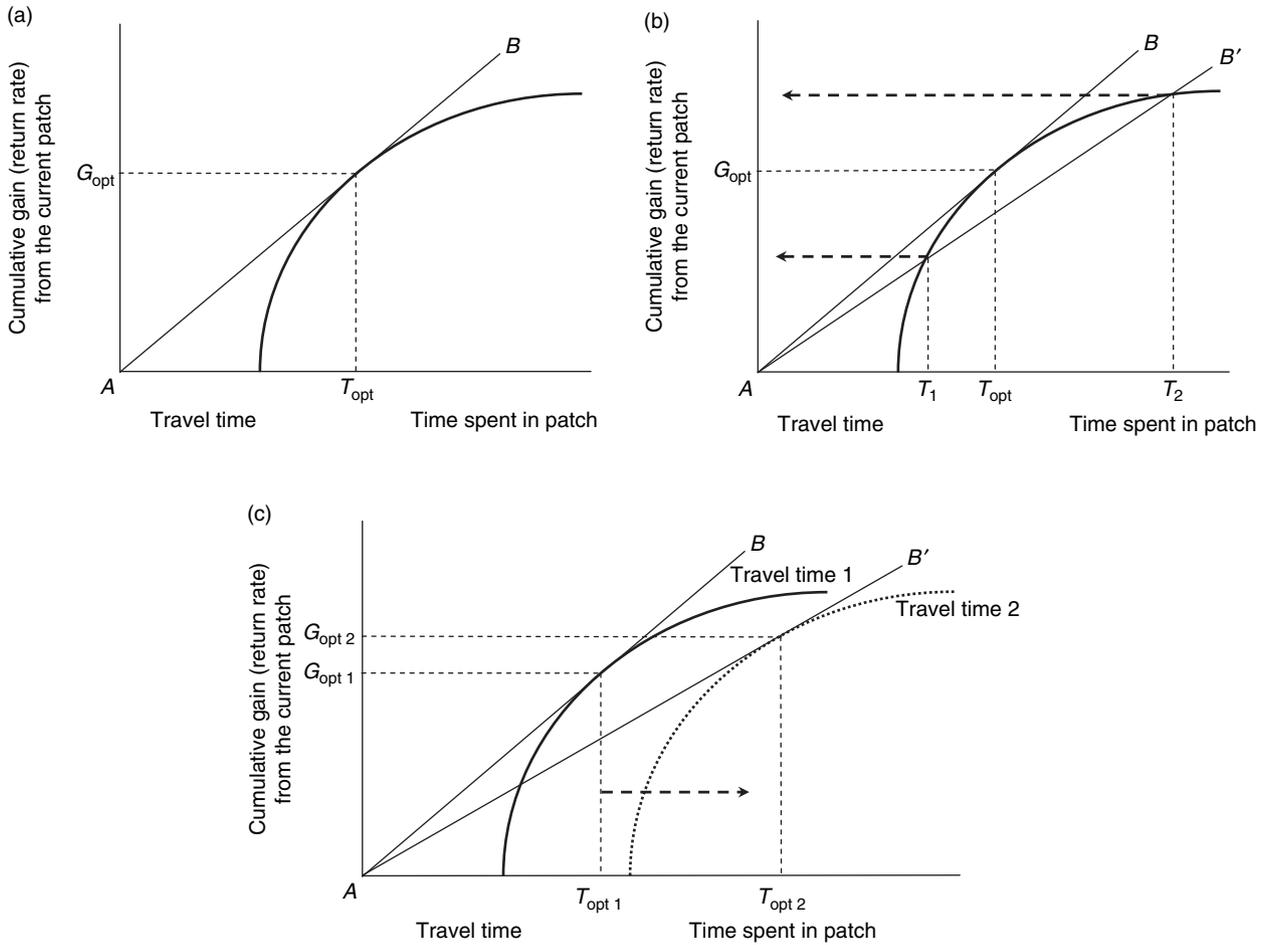
Figure 4 The marginal value theorem yields the 'giving-up time' when an individual should leave its current foraging patch. (a) As an individual forages, its cumulative fitness gain gradually slows down as food becomes scarcer in the patch and food items take longer to find. An individual should aim at maximizing the net rate of fitness (or energy) gain, including time during which it cannot feed because it travels between patches. The rate of fitness gain corresponds to line $A–B$. The steepest slope line (gain/time), which maximizes the rate of energy gain, corresponds to the tangent line to the gain curve. When time on the patch reaches the point of contact between line $A–B$ and the gain curve (T_{opt}), the individual should leave the patch. (b) An individual that leaves too early (T_1) will gain less energy per unit of time relative to the maximum (line $A–B'$). Similarly, there is no benefit in staying too long (T_2) as food items are running out. (c) When an individual should stop exploiting its current patch and leave will depend on the travel time between patches, even though the gain curve once on the patch does not change. When travel time is long, individuals should leave the patch after spending more time (T_{opt2}). Adapted from Charnov EL (1976) Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9: 129–136.

can be derived from finding a resource item, and (2) the individual's *a priori* knowledge about the environment (**Table 1**).

Breeding Habitat Selection

Individuals will also have to make a series of habitat choices for breeding. As for foraging, breeding requires availability of high-quality food resources necessary for offspring development, but also many other resources affecting breeding success, in particular the presence of mates and availability of safe breeding sites (**Figure 6**). In some species, decisions made during the course of breeding are sequential in time and space, and made independently based on different criteria. In other species,

all resources have to be secured simultaneously, which may generate tradeoffs between optimal choices for each resource. In many species, the number of breeding attempts is limited over an individual's lifetime, because breeding involves longer timescales than foraging (up to several years), and/or is a seasonal activity implying yearly timescales. Thus constraints associated with breeding habitat selection often differ from foraging habitat selection. Habitat choice may vary depending on the type of breeding site and species breeding ecology, and can occur at variable spatial scales, both in absolute values (from millimeters for some parasites to hundred of kilometers for large vertebrates), and relative values, depending in particular on the spatial range used by a given species.
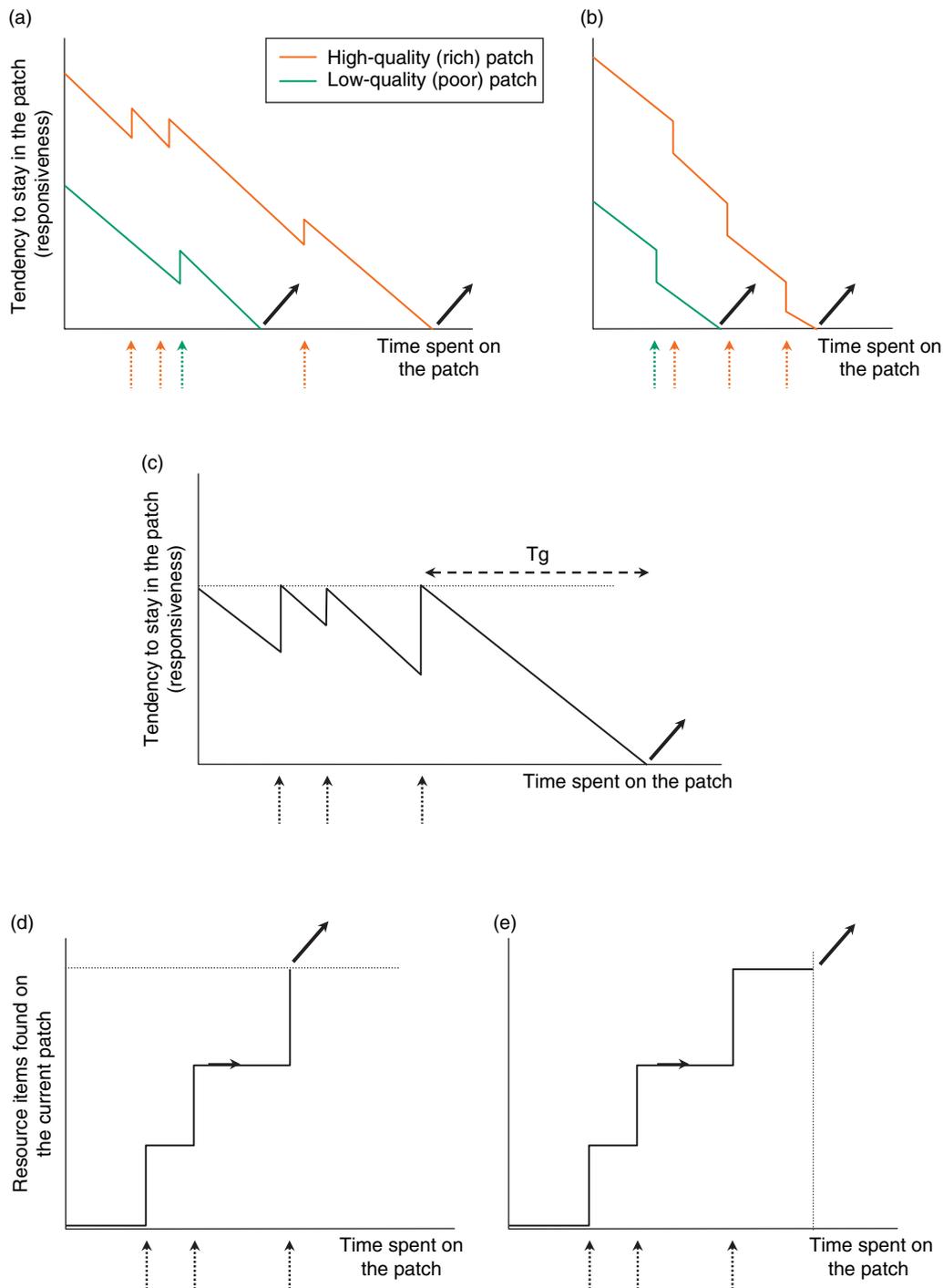
Figure 5 Patch-departure decision rules in discrete foraging environments. When resources are not distributed evenly but are aggregated in patches whose size is not *a priori* known, individuals can adopt several simple rules for deciding when to stop exploiting their current patch and leave for another patch (black arrows). Dashed arrows indicate when resources items are found by individuals. The probability to stay in the current patch, also called responsiveness, is shown depending on time spent in the patch. When the probability to stay in the current patch drops below a critical threshold, the individual leaves the patch. (a) Incremental rule; (b) decremental rule; (c) giving-up-time rule (giving-up time: Tg); (d) fixed-number rule; (e) fixed-time rule. (a, b) Adapted from Waage JK (1979) Foraging for patchily distributed hosts by the parasitoid *Nemeritis canescens*. *Journal of Animal Ecology* 48: 353–371; and Van Alphen JJM, Bernstein C, and Driessen G (2003) Information acquisition and time allocation in insects parasitoids. *Trends in Ecology and Evolution* 18: 81–87. (c) From Stephens DW and Krebs JR (1987) *Foraging Theory*. Princeton, NJ: Princeton University Press. (d, e) From Iwasa Y, Higashi M, and Yamamura N (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* 117: 710–723.

Table 1 An overview of the different rules for patch-departure decisions in the context of foraging habitat selection, and the conditions in which each rule is likely to be selected for in terms of type of environmental variation in patch quality (i.e., spatial distribution of resource items) and individuals' knowledge on the environment. All proximate rules assume that individuals cannot *a priori* assess patch quality upon entering the patch

Patch-departure decision rule	Conditions in which the rule will be selected for
Ultimate mechanism	
Marginal value theorem	
Leave patch if when the instantaneous intake rate from the current patch falls below the mean intake rate in the environment	
Proximate mechanisms	
Incremental rule	
Initial probability to stay on patch depending on its quality (size); probability to stay decreases linearly with unsuccessful time on patch; each resource item found adds an increment to the current level of probability to stay; leave patch when threshold probability is met	High variability of patch quality (aggregated spatial distribution of resource items) Limited individual knowledge about patch size
Decremental rule	
Initial probability to stay on patch depending on its quality (size); probability to stay decreases linearly with unsuccessful time on patch; each resource item found subtracts a decrement to the current level of probability to stay; leave patch when threshold probability is met	Low variability of patch quality (evenly dispersed spatial distribution of resource items) Good individual knowledge about patch size
Giving-up time rule	
Leave patch if time since last resource item found exceeds a given threshold	High variability of patch quality (aggregated spatial distribution)
Fixed-number rule	
Leave patch when a fixed number of resource items has been found	Low variability of patch quality (constant number of resource items per patch)
Fixed-time rule	
Search patch for a fixed period of time and leave patch independent of the number of resources items found	Poisson distribution of number of resource items per patch

Other Habitat Selection Behaviors

Individuals have to choose a habitat or patch in many other situations. In species where mating occurs in a different place than the remaining of breeding activity (e.g., lekking species), individuals have to select an optimal displaying habitat or patch, and within the patch, an optimal site, for example, close to a dominant male, or within a light spot in low-light-intensity environments. For instance, if visual signals are used in mate choice, the environment chosen to display can affect mating success because signal appearance depends on the joint effect of ambient light and individual's reflectance spectra (**Figure 7**). Similarly, individuals may have to choose among alternative resting habitats or patches. In this case, the main resource is a safe site from predators or a site allowing individuals to optimize energy expenditure (e.g., against cold or rain).

Migration can be considered as an extreme form of habitat selection, when individuals change habitat because resource availability is seasonal while individuals' requirements remain unchanged. However, migration behavior is a fixed habitat selection process, individuals changing habitat similarly year after year. During migration, individuals will choose stopover areas, but this choice can be considered as classical foraging habitat choice, constraints of which include energy requirements and costs of long-distance flights.

Differences between Choices: Spatiotemporal Scales Involved, Tradeoffs

Habitat selection shows fundamental differences depending on the activity considered, in particular in spatiotemporal scales involved. Estimating a foraging patch quality may take only up the time to try to find a food item (**Figure 5**). The equivalent rule for assessing a breeding patch quality implies attempting to breed to obtain information on expected breeding success in this patch, thus spending time and energy for one breeding attempt there, which may represent a significant portion of life span. In other words, foraging decisions are more dynamic than breeding habitat decisions. Breeding habitat choice may occur only once in life, when individuals decide whether to stay on or leave the natal site (natal site fidelity vs. dispersal). In mobile iteroparous species, individuals can change breeding sites between breeding events (breeding dispersal), but in many species, once the breeding place has been selected, individuals remain on that place for the whole breeding season.
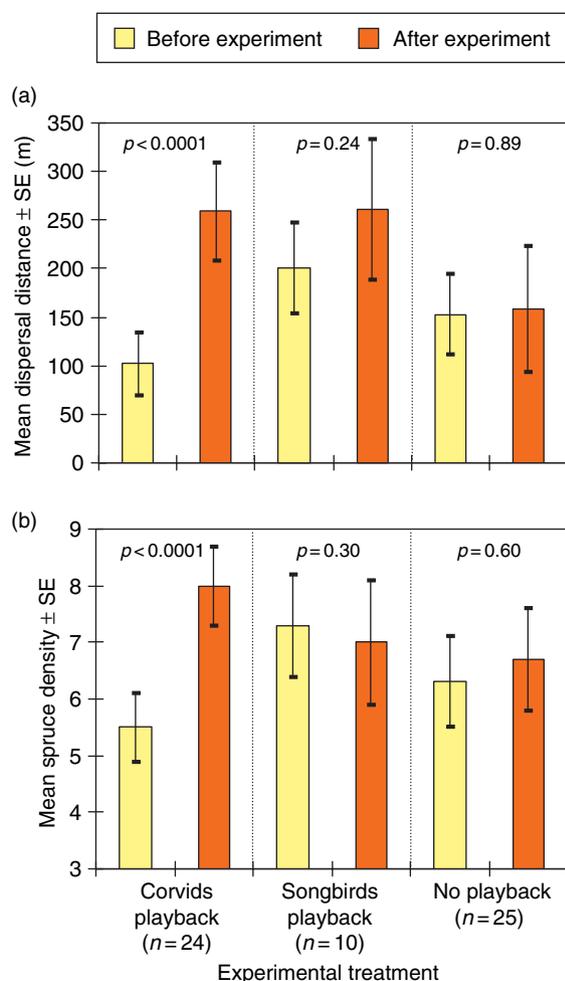
Figure 6 An example of breeding habitat selection. Influence of the perceived nest predation risk on (a) dispersal distance and (b) nest site preferences in Siberian jays (*Perisoreus infaustus*). When exposed to nest predator playbacks (corvids) compared to control playbacks (songbirds) or no playback during breeding, individuals changed their breeding site choice in the following year. Data from Eggers S, Griesser M, Nystrand M, and Ekman J (2006) Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society London Series B* 273: 701–706.

Selecting a habitat or patch often implies different habitat requirements for different activities, and may thus follow different decision rules. However, different types of habitat selection may strongly interact and therefore be traded off against one another, for instance, in species searching for food and reproductive sites simultaneously. Even when selecting a breeding and foraging location are distinct activities during the life cycle, selecting a breeding habitat constrains foraging during the whole breeding period, especially in species spatially constrained during reproduction, for example, sessile and territorially breeding species. Furthermore, breeding habitat choice is often strongly linked with mate choice,

which implies that constraints linked to sexual selection also influence breeding habitat choice, while they are unlikely to influence foraging habitat choice.

How Select a Habitat?

The Use of Information

To choose between alternative habitats or patches, individuals have to assess the relative quality of (i.e., the expected fitness for) each alternative. Choosing a habitat or patch thus implies gathering and using *a priori* information on environmental variability, and this information may be critical. Due to the strong selective pressures on habitat selection, the use by individuals of any kind of information allowing them to improve their choice should be favored. Therefore, the existence of information-based habitat choice behaviors may be expected. This raises the questions of which type of information should be used, and how individuals sample the environment and acquire information. In theory, individuals should evaluate all characteristics affecting the success of the activity considered in each site. This could clearly become prohibitive in terms of time and energy when many factors influence this activity independently or at different moments. Therefore, individual strategies for choosing a habitat or patch based on cues integrating the effect of various factors on expected fitness, or that mix different information, may be especially favored.

What Defines Information, Its Value, Quality, and Reliability?

To be informative about habitat or patch quality, a cue should allow individuals to predict reliably their expected fitness in this habitat or patch and compare alternative patches. This depends on several factors:

1. Temporal predictability of habitat quality between the time of information gathering and use is one of these factors (**Figure 8**); in seasonally breeding species, predicting environmental conditions from one year to the next may be easier than from the beginning to the end of the breeding season.
2. Degree of covariation between the cue and environmental variation is also important: an informative cue will in particular reflect environmental variation without time delay. Furthermore, the standard error of the cue measurement should be low compared to environmental variation; this will be the case when the cue is assessed on large samples.
3. Reliability of the cue as reflecting environmental variation is also one of the factors influencing information value. In particular, if the cue is linked to conspecifics' activity, they should not be able to affect it to provide
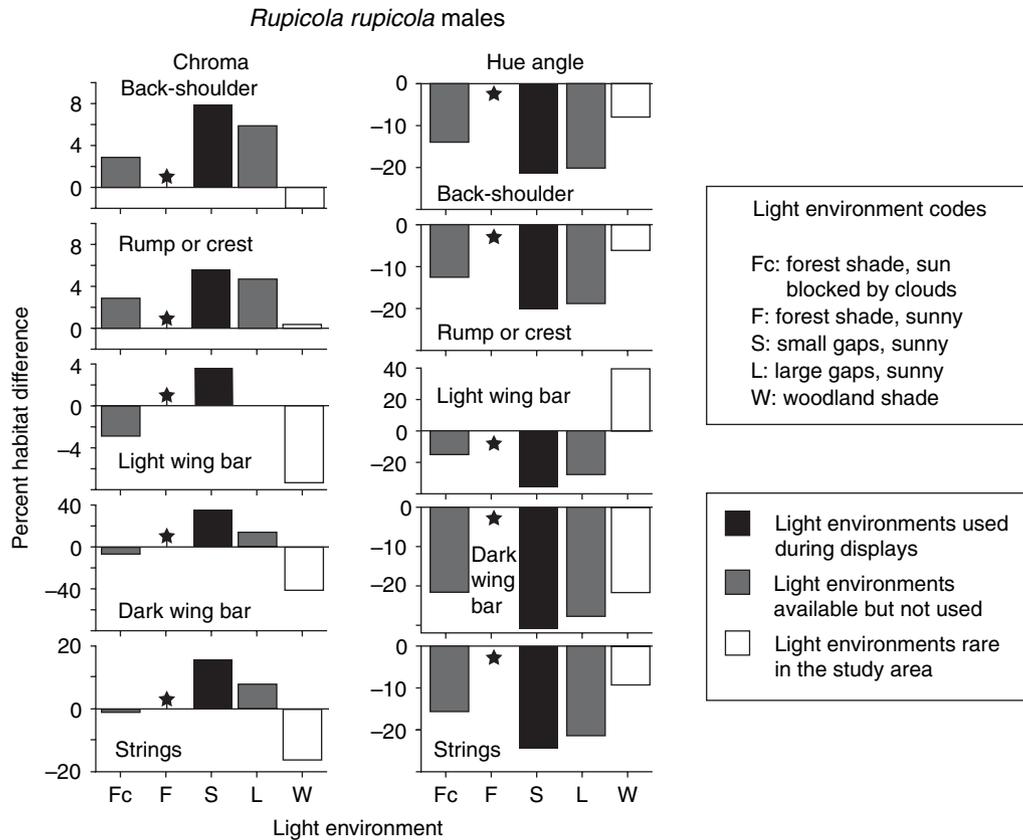
Figure 7 Display site selection by a neotropical forest-dwelling, lekking bird species, the cock-of-the-rock *Rupicola rupicola*. Forests exhibit a mosaic of spectral environments arising from both vegetation cover and weather. Males display to females both in sunny forest shade (F) and small gaps (S), and these two spectral environments show the highest percentage difference (F taken as standard, indicated by a star) with respect to chroma and hue angle for each male color plumage element (shoulder, chest, wing, etc.). Cock-of-the-rock males therefore select for displaying the two light environments that illuminate different parts of their plumage and maximize the visual contrast during displays. From Endler JA and Théry M (1996) Interacting effects of lek placement, display behaviour, ambient light, and color patterns in three neotropical forest-dwelling birds. *American Naturalist* 148: 421–452.

false information; also, phenotype– or genotype–environment interactions should be limited.

4. Integrative power of the cue, which should be closely related to fitness, is another factor.
5. Easiness of cue assessment, that is, costs of acquiring or gathering information, which depend on (a) direct costs of sampling the environment (e.g., reduced survival due to predation or aggressive interactions) and (b) indirect costs (e.g., time lost in sampling and not used for other activities), is also factored in.

Subsequent costs may also be paid through competition between individuals using the same information and thus making the same choice. The costs (and thus the value of information) will depend on both species biology and spatiotemporal environmental variation of habitat quality, for example, individuals' mobility, length of the breeding period, and synchronization of breeding events among and within patches. In conclusion, the value of information will depend on the balance of information-gathering costs and benefits gained from its use.

Different Types of Information for Habitat Selection

Depending on species biology and activity considered, individuals can use many types of information, ranging from physical and biological habitat characteristics to conspecifics.

Nonsocial cues

Individuals may directly evaluate potential resources and constraints affecting success in a given activity (e.g., food availability, parasitism load, predator presence – **Figure 6**). If success is mainly linked to one factor, then this strategy should prove efficient to assess habitat quality. However, when this factor is difficult to assess, when many factors affect success, or when information on some factors is not available at the time of information gathering, an alternative is to use indirect cues revealing the effect of important factors, for example, chemical compounds revealing the presence of predators. Individuals can use search images of suitable habitats acquired during development (imprinting) or later (learning).
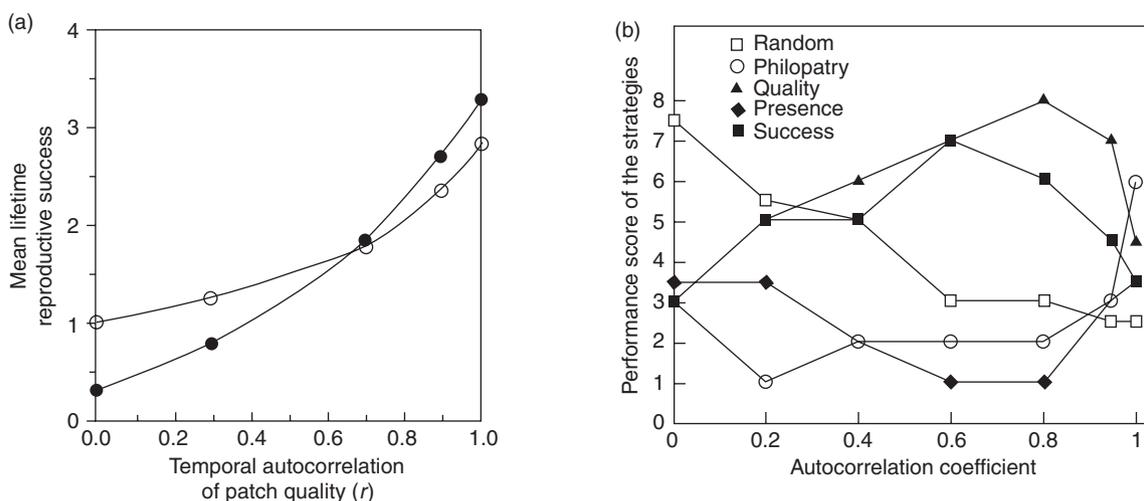
Figure 8 The value of 'public information', that is, the local reproductive success of conspecifics, for breeding habitat selection depending on environmental temporal predictability. In most seasonally breeding species, this cue will be available at the end of the breeding season, and can therefore only be used in the next year. It will thus be valuable only if the environment is autocorrelated from one year to the next. (a) In an optimality model, individuals choosing their breeding patch according to local reproductive success in the previous year (closed dots) achieve a higher lifetime reproductive success compared to individuals settling at random on a patch (open dots) only when the level of temporal autocorrelation of the environment is high. (b) Similarly, in a game theory model, strategies based on local reproductive success ('quality' and 'success') are selected for only when the level of temporal autocorrelation of the environment is sufficiently high. (a) From Boulinier T and Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology* 11: 505–517. (b) From Doligez B, Cadet C, Danchin E, and Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* 66: 973–988.

Individuals may also use as information source their own experience and history, in particular their own performance in the activity considered in the habitat or patch, called personal information (and sometimes also private information, despite that other individuals can access it – **Figure 9**). In the context of foraging, different strategies involve gathering information via direct environment sampling by individuals, using in particular trial-and-error tactics (stay after success, leave after failure). Differences in timescale between foraging and breeding decisions imply that trial-and-error strategies, which can be optimal in foraging, are unlikely to be selected for alone in breeding habitat choice, because they would imply settling at random to breed and using only the breeding success achieved to decide about future habitat choice. This might be very costly when the total number of breeding attempts is limited, and personal information in the case of breeding habitat selection will often be mixed with other sources of information. Philopatry, that is, fidelity to the natal site, can be considered as a form of personal information use: individuals choose a site whose quality has allowed their own growth and survival.

Social cues

Conspecifics can also be used as a source of information about local habitat quality, that is, social information, because they share the same needs. Social information may be provided either intentionally through signals (communication), or inadvertently (inadvertent social information), when individuals monitor the behavior and performance of their conspecifics. When individuals use social information, they benefit in particular from environment sampling performed by others. Individuals can be expected to use social information more often for breeding than foraging habitat choice, and the importance of this information for breeding habitat choice has recently been emphasized (**Figure 10**).

Conspecifics' presence on a habitat patch as an information source has received much attention (social attraction process). It can reveal good enough conditions for a local population to persist (**Figure 10**). However, the mere presence of conspecifics may be misleading because the correlation between local density and habitat quality can prove weak in certain conditions. Conspecifics' activity and their success may better reveal habitat quality. Where conspecifics are the most successful can indicate where an individual is the most likely to be successful itself. Conspecific success integrates in a single parameter the effect of all components of environmental quality, including social interactions (**Figure 10**). It can also be more precise than personal information when based on large samples (e.g., many conspecifics), and when phenotype–environment interactions are limited. The
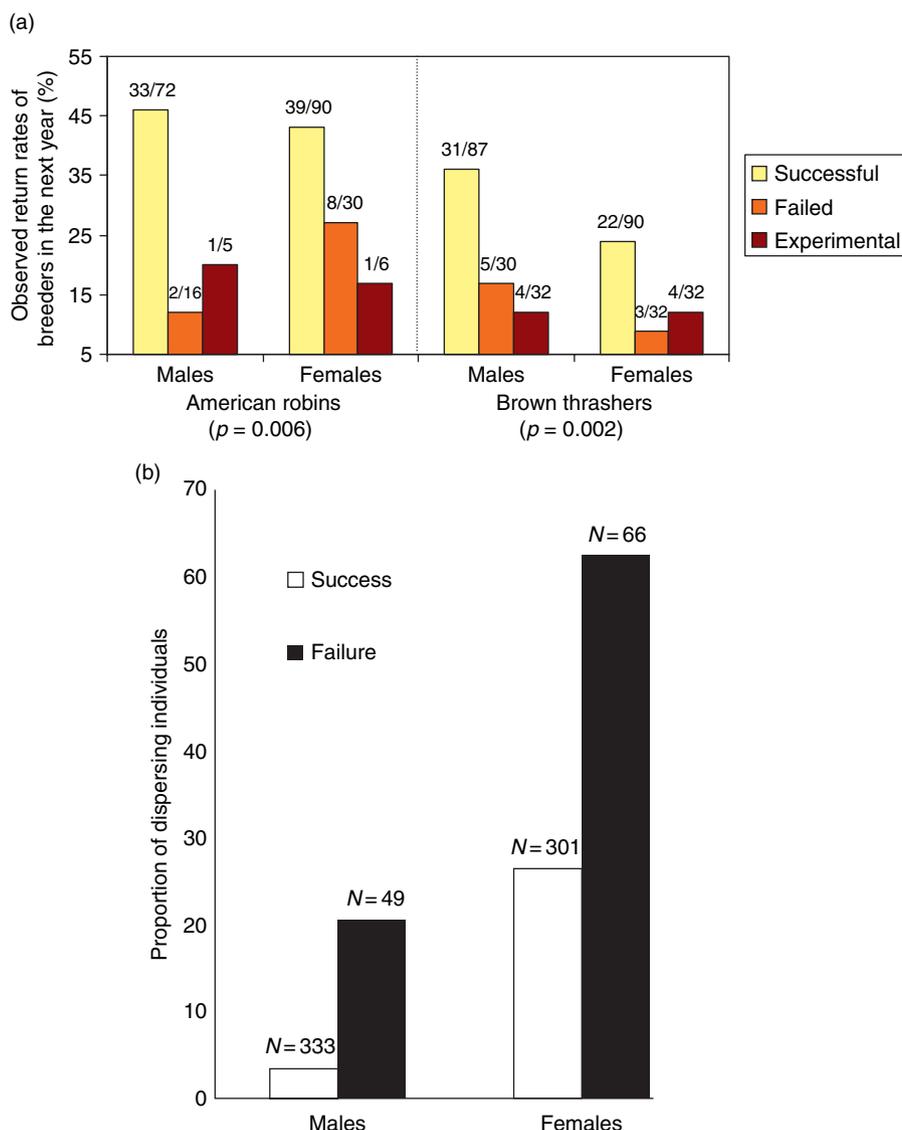
Figure 9 Influence of personal information (individual's breeding success) in subsequent breeding habitat choice in (a) American robins (*Turdus migratorius*) and brown thrashers (*Toxostoma rufum*), and (b) collared flycatchers. Failed (naturally or experimentally) breeders are more likely to disperse to another patch in the following year compared to successful breeders. Individuals use their own reproductive performance as a cue to assess the current local breeding habitat quality and adjust their breeding patch choice in the next year. (a) Data from Haas CC (1998) Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. *Auk* 115, 929–936. (b) From Doligez B, Danchin E, Clobert J, and Gustafsson L (1999) The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* 68: 1193–1206.

information derived from the performance of other individuals sharing ecological requirements has been called public information, in contrast to personal information.

The use of social information can be extended to heterospecifics, provided that they share the same needs (e.g., food or breeding sites), leading to interspecific social attraction or the use of heterospecific public information (**Figure 10**). Because their characteristics will slightly differ from individuals of the focal species, they could even provide additional information compared to conspecifics.

Individuals are likely to combine and use several information sources, in order to refine their assessment of local habitat quality and adjust their future decisions, depending on which factors affect fitness and relative costs of gathering each information (**Figure 11**).

Sampling the Environment and Gathering Information: Prospecting

Information gathering about relative habitat quality via prospecting behavior involves sequential visits of potential occupied or nonoccupied patches or sites by an individual
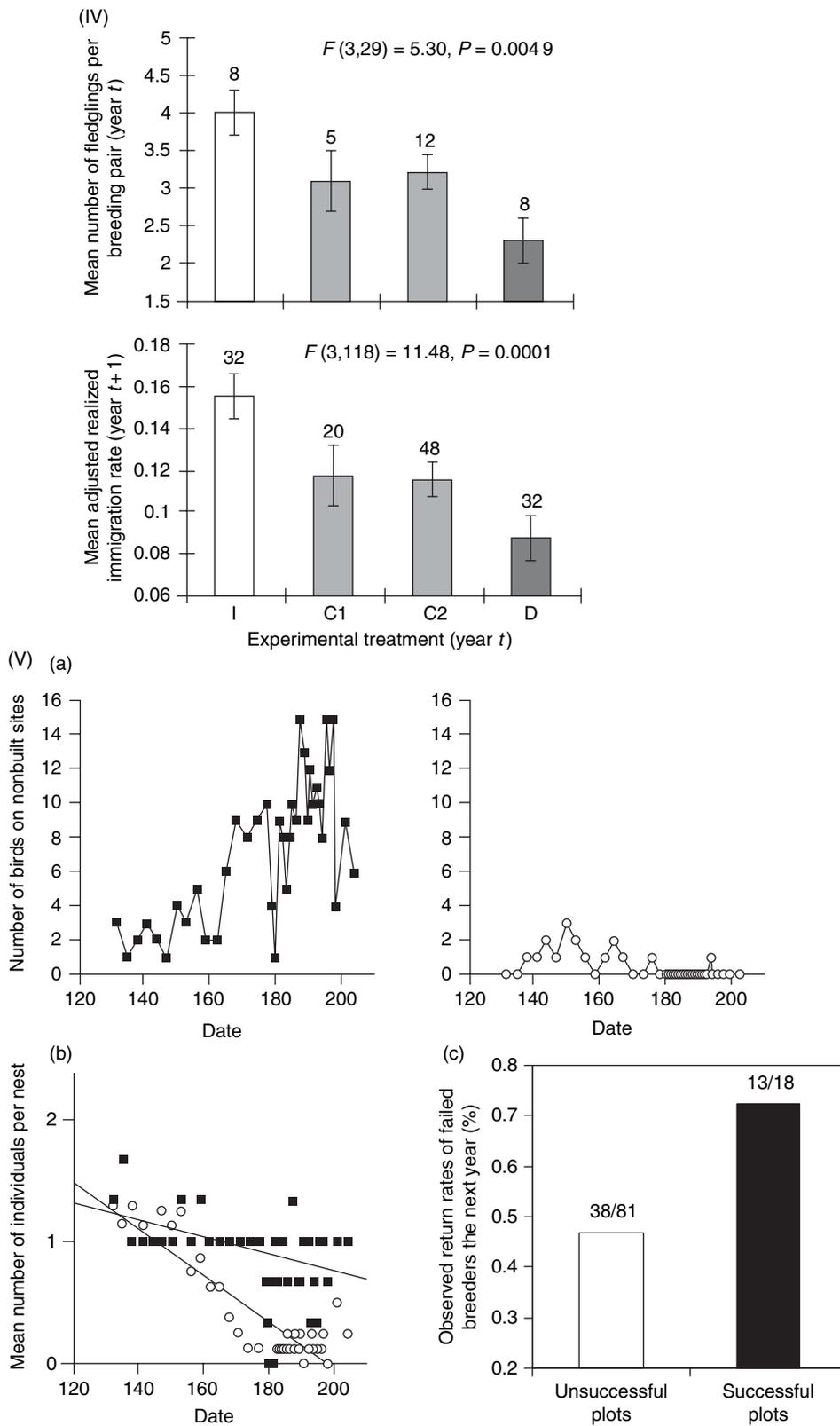
(I)

(II)
(a)

(b)

(III)
(a)

(b)

(IV)

$F(3,29) = 5.30$, $P = 0.0049$

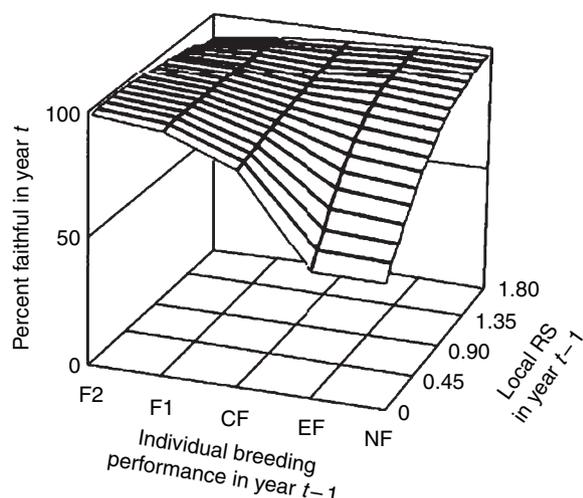(V) (a)
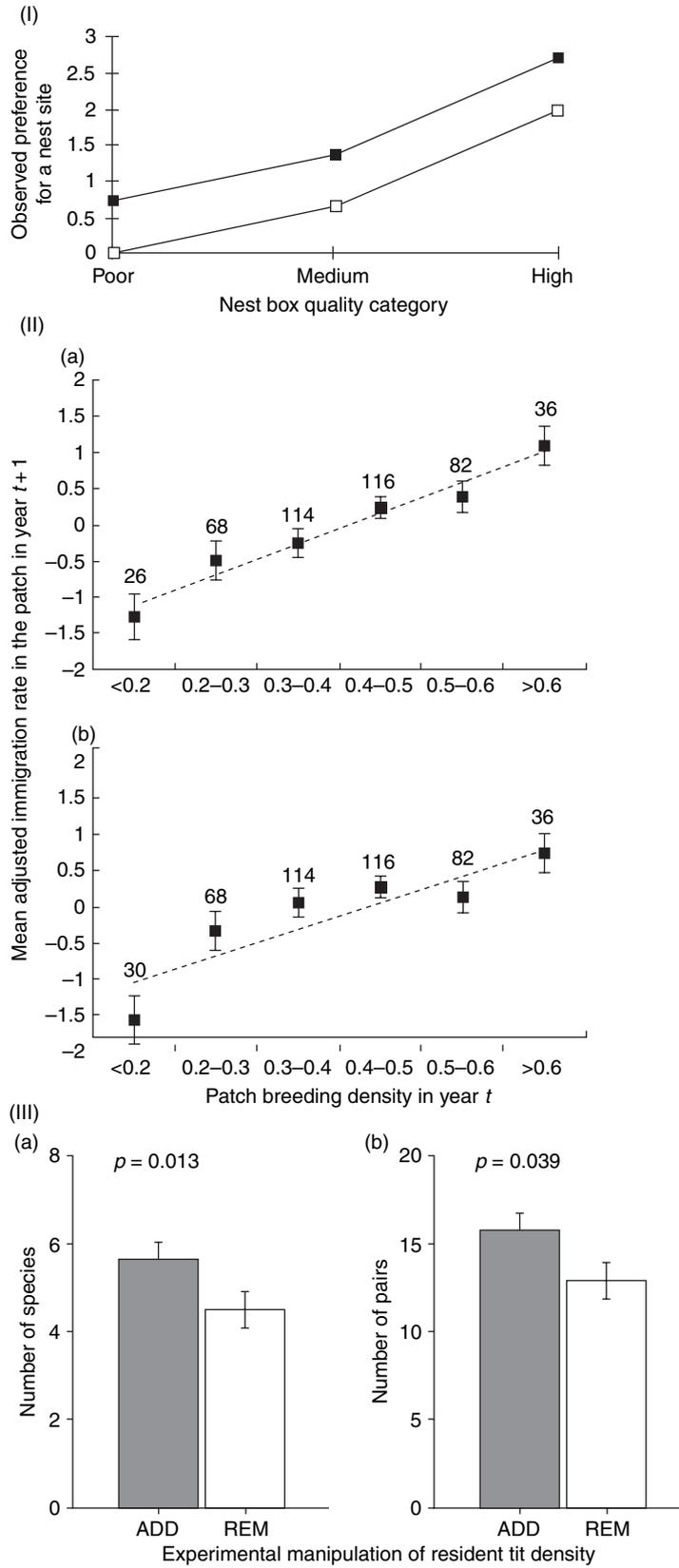
Figure 10 (*Continued*)

Figure 11 Combining several sources of information for breeding habitat choice. In the black-legged kittiwake, the fidelity probability of breeders depended on both personal information (i.e., individual reproductive success) and public information (i.e., local reproductive success (RS) of conspecifics on the patch) in the previous year. Individual reproductive success decreases from F2 (high success) down to NF (nest failure: no eggs laid). Local reproductive success: average number of chicks fledged per nesting pair on the patch. Personal and public information significantly interacted. Successful individuals (F2 and F1) were always highly faithful to their breeding patch, while fidelity of early failed individuals (NF and EF) increased with local success. Thus, individuals used both personal and public information to decide whether to emigrate, but prioritize the different sources of information: public information was used only after breeding failure. From Danchin E, Boulinier T, and Massot M (1998) Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* 79: 2415–2428.

that does not currently feed or breed there (called a prospector). Despite the major impact of prospecting on habitat choice, data on prospecting remain fragmentary. Prospectors on breeding patches are usually immature individuals before recruitment, and nonbreeding or unsuccessful adults, which are likely to be looking for a breeding site for the following year. However, the links between prospecting, type of information gathered by prospectors, and subsequent habitat choice are still poorly investigated. Constraints acting on prospecting can however determine which types of information are available to individuals, and thus which habitat choice strategies can evolve. Prospecting may also shape the evolution of life-history traits such as age at first breeding when individuals have to prospect before settling for breeding.

Constraints on Habitat Selection

Habitat choice involves two important steps: (1) deciding whether to leave or stay on the current habitat or patch; (2) if individuals decide to leave, choosing where to settle next. These two sets of decisions may be based on different criteria, and be either independent or linked: individuals may decide to leave before having decided where to settle next; alternatively, they may decide to leave because they have already chosen their next patch. Choices can occur on repeated occasions, and thus be increasingly shaped by personal experience, except for breeding habitat selection in sessile species. Habitat choice is thus a complex process constrained by many

Figure 10 Examples of the use of different types of social information for breeding habitat selection: (I and II) presence of conspecifics, (III) presence of heterospecifics sharing the same needs, (IV and V) local reproductive success of conspecifics. (I) Naive house wren males (*Troglodytes aedon*) preferred to settle in nest boxes of higher quality (as measured by previous breeding success in the box), but also close to the nearest occupied box. Black squares: boxes located ≤70 m from the nearest occupied box (open squares for >70 m). (II) Immigration rate of new breeders in a patch strongly positively increased with patch breeding density in the previous year, for both (a) experienced (≥2 years old) and (b) naive (yearling) collared flycatchers. (III) The number of migrant passerine bird species and densities of migrant individuals were lower in patches where the density of heterospecific resident tit (*Parus*) species was decreased (REM) by removing individuals than in patches where it was increased (ADD) by releasing them. (IV) Immigration rate of collared flycatcher breeders was higher in patches where the mean number of fledglings had been increased locally (by adding nestlings – patches I) in the previous year compared to control (C1 and C2) patches (unchanged mean fledgling number), and higher in control patches compared to patches where the mean fledgling number had been decreased locally (by removing nestlings – patches D). (V) In the black-legged kittiwake, (a) prospecting and (b) nest attendance by failed breeders were higher on patches where local success was unchanged (black dots) than where it had been experimentally decreased by removing eggs (open dots), and, in the following year, (c) failed breeders were more likely to return to breed on the same patch in patches where success was unchanged (black bar) compared to decreased patches (open bar). (I) From Muller KL, Stamps JA, Krishnan VV, and Willits NH (1997) The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* 150: 650–661. (II) From Doligez B, Pärt T, Danchin E, Clobert J, and Gustafsson L (2004) Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* 73: 75–87. (III) From Forsman JT, Mönkkönen M, Helle P, and Inkeröinen J (1998) Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. *Oecologia* 115: 278–286. (IV) Reproduced from Doligez B, Danchin E, and Clobert J (2002) Public information and breeding habitat selection in a wild bird population. *Science* 297: 1168–1170, with permission from AAAS. (V) From Boulinier T, Yoccoz NG, McCoy KD, Erikstad KE, and Tveraa T (2002) Testing the effect of conspecific reproductive success on dispersal and recruitment decisions in a colonial bird: Design issues. *Journal of Applied Statistics* 29: 509–520.

parameters linked to: (1) species characteristics, in particular cognitive (spatial and temporal memory) and movement capacities (maximal movement rate or distance, especially when individuals have to travel across unsuitable habitat – arrows in **Figure 1**); (2) species life-history strategy and tradeoffs involved (investment in different activities, in particular prospecting vs. breeding; tradeoffs in choosing multiusage sites, in particular year-round territories); (3) individuals' characteristics and interindividual differences in the ability to exploit the environment (phenotype– or genotype–environment interactions), in habitat preferences (through imprinting or habitat training due, for example, to acquired parasite resistance), or in selective pressures (e.g., sexual selection depending on individual's sex); and (4) environment variation (e.g., temporal predictability, spatial variation patterns).

Testing the Existence of Habitat Selection Processes

Processes, that is, mechanisms, of habitat choice have to be distinguished from patterns of space use, that is, distribution of individuals in the environment resulting from individual decisions. Patterns of individuals' spatial distribution or variation in fitness are often used to infer habitat choice processes by individuals, because determining whether habitat selection occurs can be difficult. Empirical studies often analyze habitat choice processes by comparing site characteristics and patterns of site use in different types of habitats. Occupied sites are expected to be of higher quality than unoccupied or randomly picked up sites if habitat choice occurs. However, the same patterns can result from different processes, and from processes other than active habitat selection by individuals.

A widely used concept is the ideal free distribution (IFD), defined as the distribution of individuals among habitat patches expected under the assumptions that individuals (1) distribute themselves so as to optimize their fitness, (2) are free to move among habitat patches, that is, without any cost or constraint, and (3) have a perfect (ideal) and instantaneous knowledge of the relative quality of habitat patches and local density dependence function. At equilibrium, (1) mean individual fitness is equal on all patches because individuals are distributed among patches proportionally to the relative quality (availability of resources) of each patch and (2) individuals cannot increase their fitness by changing patch (**Figure 12**).

More realistic refinements of the IFD model including (1) different forms of density dependence (e.g., nonmonotonic density-dependent functions such as Allee effects) and (2) interindividual differences in competitive ability (allowing some individuals to monopolize resources and

thus achieve higher fitness than others: ideal despotic or dominant distribution (IDD)) have been proposed, but the IFD represents a null model describing the spatial distribution of individuals in the environment that maximizes fitness at the population scale given the distribution of patches, and to which distributions generated via different habitat choice processes incorporating constraints on information accessible to individuals (the ideal assumption) and their movements (the free assumption) can interestingly be compared (**Figure 13**).

Inferring habitat choice solely from patterns of habitat use by individuals can be misleading because high densities may be observed on low-quality patches, for instance, because of constraints for individuals in obtaining reliable information about potential habitat patches quality. A direct investigation of habitat choice, aiming at identifying information cues and decision rules used by individuals and determining the extent to which habitat choice strategies affect fitness, is often more appropriate than indirect inferences. Such an approach links proximate factors (elements of the environment used by individuals for choosing in a mechanistic way) and ultimate factors (evolutionary causes of individual choices, that is, linked to the relative fitness of individuals adopting different habitat choice strategies) involved in habitat choice.

Individual and Population Implications of Habitat Selection

Spatial Distribution of Individuals and Evolutionary Consequences

Habitat choice directly affects the distribution of individuals in the environment and their use of habitat patches through movement and dispersal. Individual habitat choice is thus linked to spatial aggregation patterns at the population level, and the choice of each individual may have important consequences for the rest of the population (**Figure 14**). Different habitat selection decisions, in particular foraging and breeding, will affect the dynamics of individuals' distribution in the environment, but at different timescales: foraging habitat selection is linked to short-term use of the environment, while breeding habitat choice will be directly linked to long-term persistence of local populations via reproduction and exchanges of individuals (thus genes) between populations, that is, dispersal.

Habitat choice strategies based on different information sources may generate different individuals' distributions among patches and temporal dynamics (**Figure 14**). In particular, social attraction (i.e., use of conspecifics' presence) will progressively strongly aggregate individuals on the highest-density patch, and the whole population may end up in a single patch, independently from the relative
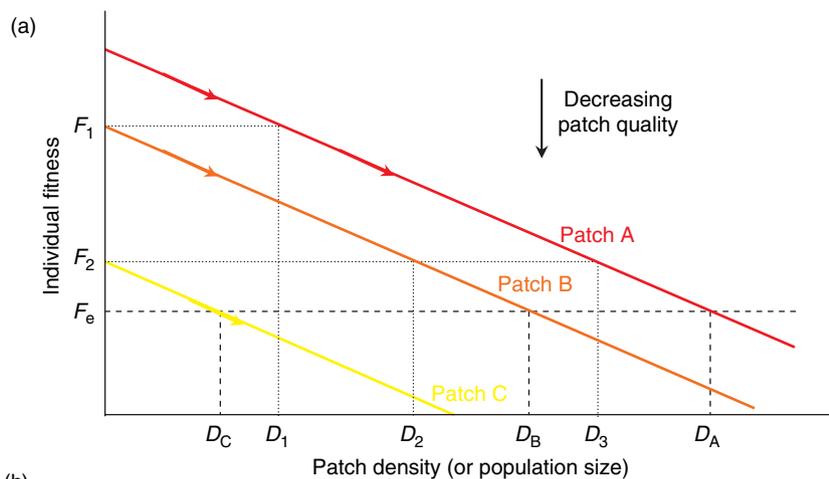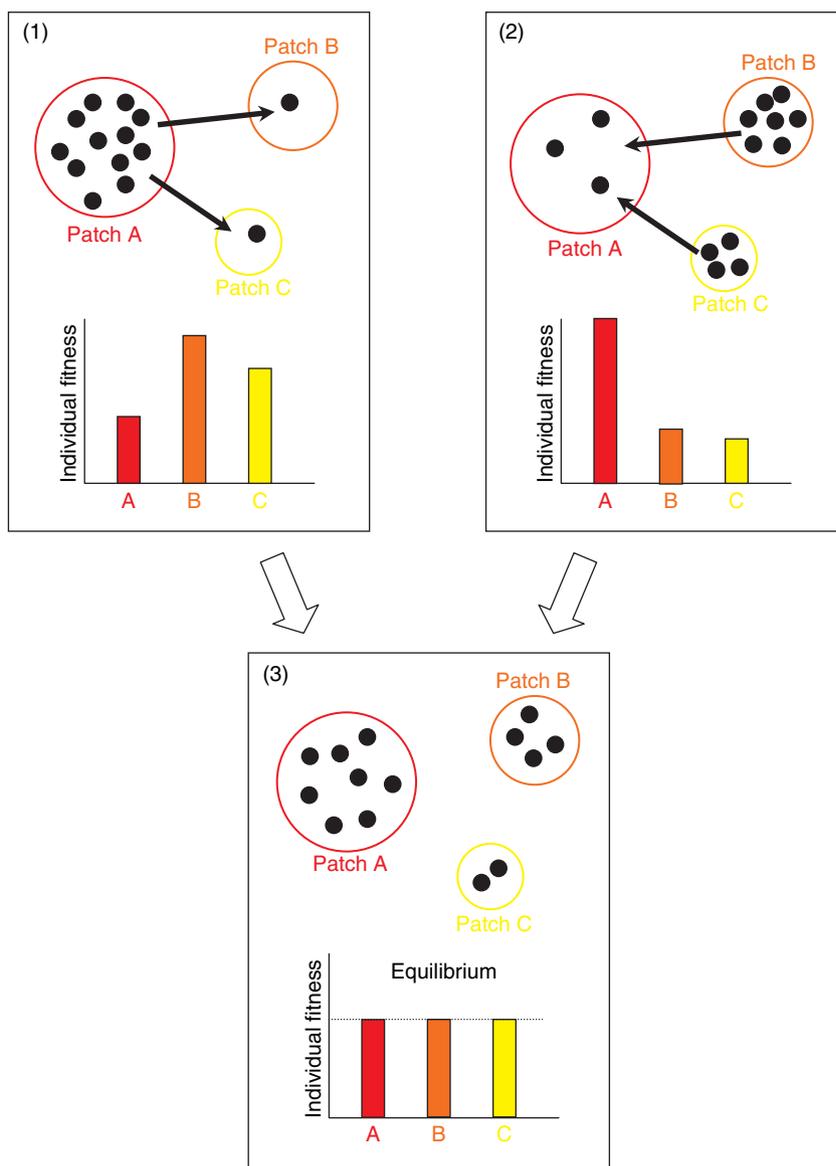
qualities of the different patches. The presence of individuals prevented from breeding because of the lack of available sites on highly occupied patches while breeding sites are available on other suitable patches can be explained by the use of social attraction for breeding habitat selection. Breeders will indeed aggregate on a fraction of suitable patches rather than colonizing empty patches, and on these occupied patches, only a fraction of the individuals manage to secure a breeding site, the rest remaining nonbreeders because of patch saturation. Constraints in habitat selection may therefore lead to the evolution of floating and queuing strategies.

Effect of habitat choice on population regulation

Simple habitat choice decision rules can also participate in site-dependent regulation of populations, through the sequential occupation of sites of decreasing quality ([Figure 14](#)). When the population increases due to high fitness on good-quality patches, an increasing proportion of individuals start settling on patches of lower quality. Thus average fitness at the population scale decreases, which reduces the overall population growth rate, and may lead the population to start decreasing. This regulatory effect is obtained simply through the variation in the mean quality of chosen and occupied sites, even in the absence of local crowding effects (i.e., negative density dependence at the individual level), that is, no decrease in fitness is observed for individuals occupying the best sites: the population growth rate varies simply because of the variation in the mean quality of occupied sites.

Habitat choice and local population viability

Individual choices are constrained by the accessibility of reliable information, and the use of suboptimal information sources may increase individuals' spatial aggregation. In a metapopulation (i.e., a set of populations connected by dispersal), individuals' aggregation on some patches leaving others empty may increase the overall extinction probability of the metapopulation by increasing the probability of simultaneous extinction of all subpopulations. In addition, if individual fitness negatively depends on local density, aggregated distributions further increase local extinction probabilities. Mixed strategies of habitat choice, using a combination of cues, or condition-dependent habitat selection strategies, may minimize extinction probability.

Evolution of sociality and coloniality

Individual strategies based on conspecific cues have also been suggested to lead to the evolution of group living. By affecting spatial distribution of individuals in the environment and thus population structure, habitat selection can lead to selective pressures favoring the evolution of group living behaviors. The use of social information for habitat choice may have led to different forms of group living, such as coloniality, since individuals using conspecifics' presence or performance for breeding site choice settle on already-occupied patches and thus aggregate breeding sites. Furthermore, feeding or breeding close to conspecifics may favor the gathering of social information on habitat quality, thus individuals may actively seek spatial aggregation to gather social information.

Conservation Biology

Through effects on the spatiotemporal distribution of individuals in the environment and population extinction probability, habitat selection behaviors have strong implications for conservation biology.

Small and fragmented populations

Threatened populations are usually small and subdivided within fragmented habitats. Habitat choice behaviors are critical for conservation issues because: (1) habitat choice strategies affect individual exploratory and prospecting movements between isolated habitat patches, which can lead to increased mortality risk depending on the degree of fragmentation; (2) the distribution and movements of individuals among habitat patches directly affect the dynamics and viability of the small subpopulations and thus the metapopulation; (3) individuals may end up settling on low-quality habitat because of constraints on mobility and information gathering, or on sites of decaying quality because of human activity. The study of breeding habitat choice is thus critical for the monitoring and management of threatened, reintroduced, or reinforced

Figure 12 The ideal free distribution. (a) Individuals start occupying the highest quality patch (patch A). As population density on patch A increases, fitness return decreases as a result of a negative density-dependence function (e.g., due to competition). When density on patch A reaches level D_1, expected fitness on patch A is equal to expected fitness on patch B, which is of lower quality but still empty. The next individuals to arrive should thus start occupying patch B, as well as continuing to occupy patch A. The same applies for patch C (level D_2 on patch B and D_3 on patch A), etc. At equilibrium (dashed line), individuals are distributed among patches (densities D_A, D_B, and D_C) so that their fitness is equal on all patches (F_e). (b) This mechanism can also operate in a closed population when local densities of individuals change as a result of demographic or environmental stochasticity. Unbalanced local densities will generate different fitness gains on different patches, due to the overexploitation of rich patches (patch A, case b1) or poor patches (patches B and C, case b2). In this case, some individuals should move to a less exploited patch, so that individual fitness as equilibrium is equal on all patches again (b3). Adapted from Fretwell SD and Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. Theoretical developments. *Acta Biotheoretica* 19: 16–36.
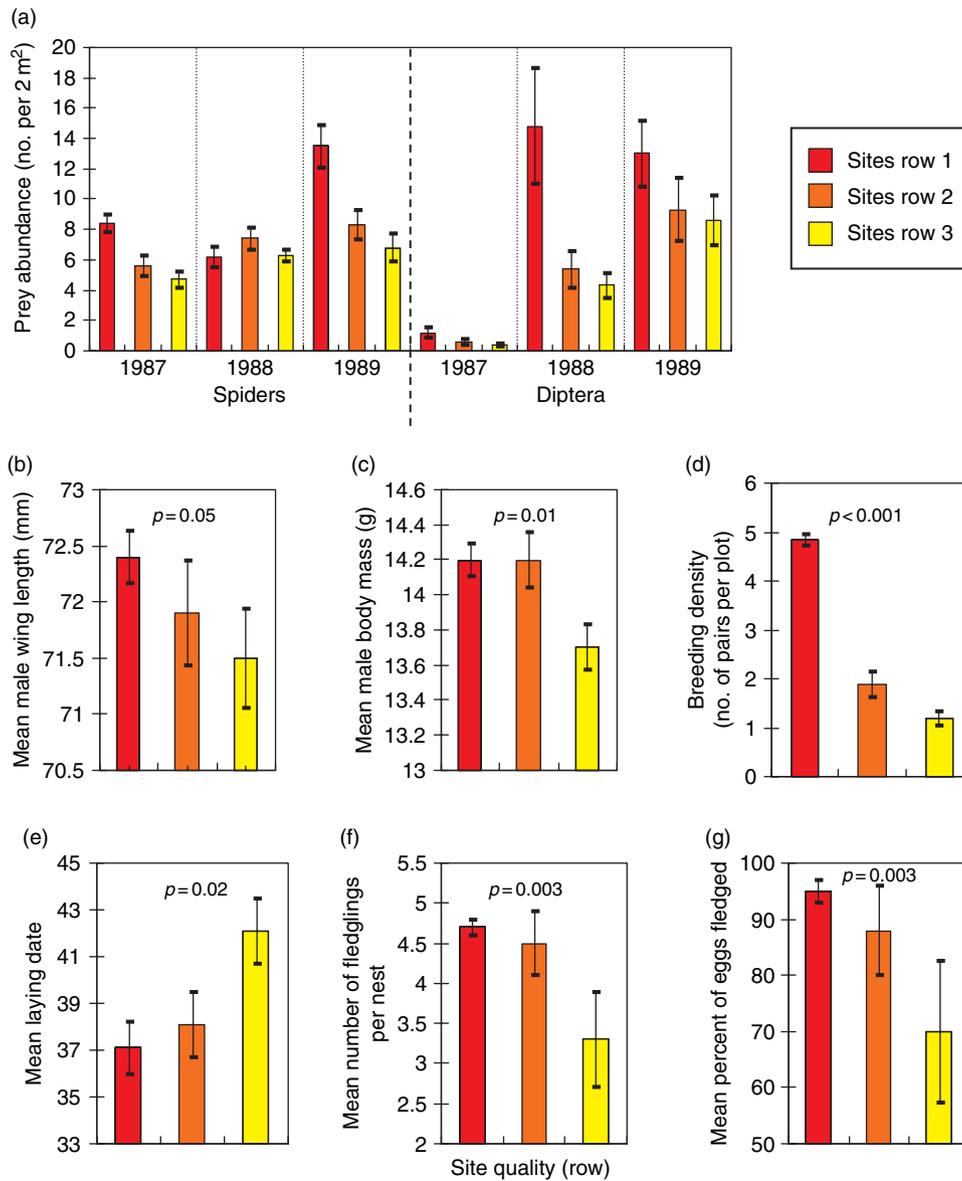
Figure 13 Testing the predictions of the ideal free and ideal dominant distribution (IFD/IDD) models in a population of prothonotary warblers. Habitat and breeders characteristics were compared between sites of varying quality. Sites differed in their relative location with respect to shoreline, with increasing distance to the shore for increasing row level. (a) Prey abundance (thus intrinsic site quality) gradually decreased with increasing site row. Breeding male (b) wing length and (c) body mass (measuring male quality), and (d) breeding densities decreased with increasing row level, i.e., decreasing site quality (no differences in females). (e) Females initiated breeding earlier in high-quality (row 1) sites compared to low-quality (row 3) sites. Finally, breeding success measured by (f) mean fledgling number and (g) percentage of eggs that produced fledglings decreased with decreasing site quality. Thus the spatial distribution of prothonotary warblers in this population followed an IDD, with higher-quality males excluding lower-quality ones from the preferred, highest-quality areas, and thereby achieving higher reproductive success. Data from Petit LJ and Petit DR (1996) Factors governing habitat selection by prothonotary warblers: Field tests of the Fretwell–Lucas models. *Ecological Monographs* 66: 367–387.

populations. Knowledge of factors affecting habitat choice has direct implications in such situations, and may greatly influence the design and monitoring of protected areas as well as the assessment of subdivided populations' viability.

Environments under human influence

Human activities can alter habitat structure and quality, and in particular break the natural correlations among habitat components. Thus, naturally selected habitat choice strategies may become maladaptive in environments modified by human activity: individuals may be lured to unsuitable patches because cues no longer reveal habitat quality when some habitat characteristics affecting fitness deteriorated but do not affect the cues used by individuals to assess site quality. Such a mismatch defines an ecological trap. Because small and subdivided
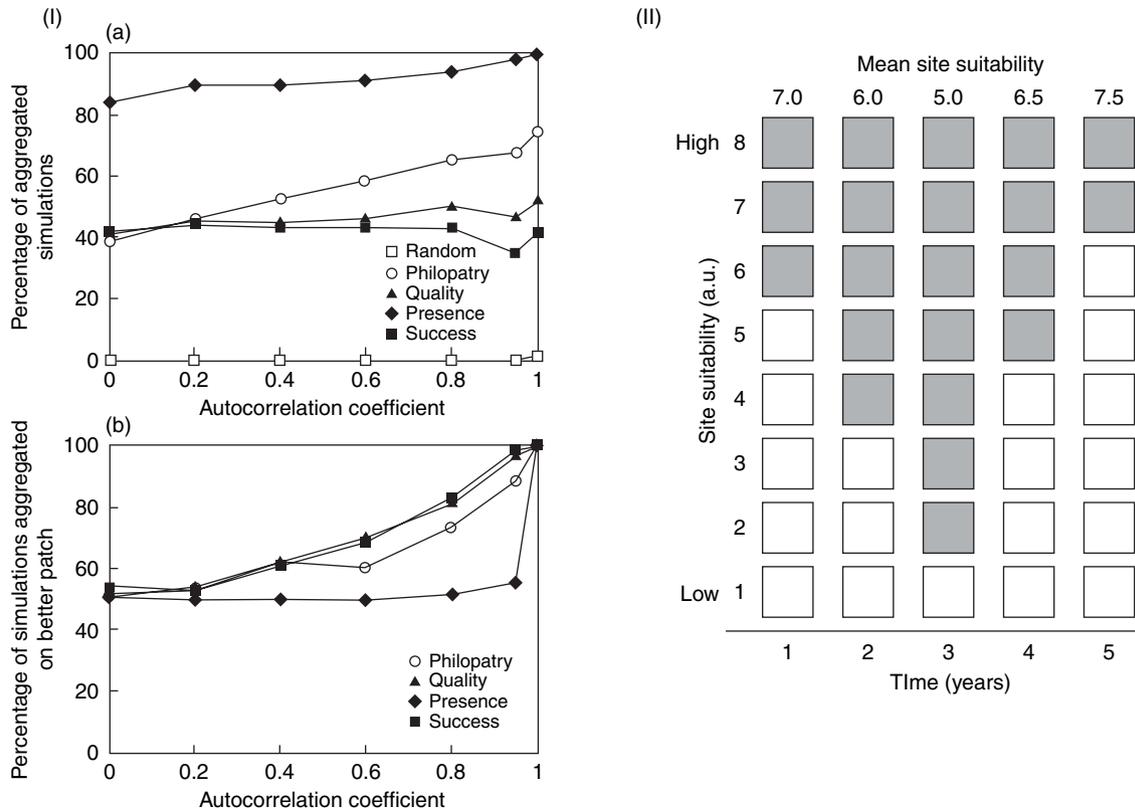
Figure 14 An illustration of population consequences of individual habitat selection behavior. (I) Spatial aggregation of individuals. Strategies of breeding habitat selection based on different types of information lead to different levels of spatial aggregation of individuals among patches (a). In particular, the use of the presence of conspecifics generates spatial aggregation far above the IFD. (b) Individuals aggregate on the best patches as environmental predictability (and thus the value of information) increases. However, when breeding success is negatively density dependent, individuals using the presence of conspecifics pay a cost via decreased success, which limits the efficiency of this strategy. (II) Population regulation via site quality. A negative feedback can be created via individual habitat selection behavior. In small populations, individuals occupy the best patches, leading to a high growth rate (year 1). When population increases, individuals start settling on sites of decreasing quality, thus mean occupied site quality decreases (years 2 and 3). Consequently, population growth is slowed (year 4). As population declines again, mean quality of occupied sites, and thus population growth, increases again (year 5). (I) From Doligez B, Cadet C, Danchin E, and Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* 66: 973–988. (II) From Rodenhouse NL, Sherry TW, and Holmes RT (1997) Site-dependent regulation of population size: A new synthesis. *Ecology* 78, 2025–2042.

populations have often greatly decreased in size in the recent past, a large proportion of potentially suitable patches may be unoccupied, but may nevertheless need to be preserved to allow individuals to move. Such situations require managing habitat in terms of metareserves aiming at protecting a habitat type independently from the current occupation by the species of interest.

Reintroduced populations

Finally, a thorough understanding of habitat choice behaviors is useful for increasing the efficiency of population reintroduction or reinforcement. The rearing conditions of individuals may affect their tendency to choose specific types of habitats, and habituation to a site can contribute to early individual settlement after release while a large mismatch between rearing and release habitats may result in individuals being unable to make optimal habitat choices. Social interactions can also be critical, such as attraction to active breeding conspecifics. Visual and/or sound decoys (e.g., mimicking successful conspecifics) can attract individuals to sites identified as suitable by managers. Decoys of predators can also be used to deter focal individuals from settling in areas identified as low quality. In other words, understanding the cues used by individuals for selecting a habitat patch allows manipulating these cues to alter individuals' choices.

See also: Competition and Behavior; Conservation Biological Control and Biopesticides in Agricultural; Cooperation; Dispersal–Migration; Mating Systems.

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