The effect of conspecifics on habitat selection in territorial species

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Summary. Despite widespread interest in habitat selection, many of the assumptions about how territorial animals choose habitats have not been tested. This study of juvenile *Anolis aeneus* lizards focuses on the relationship between the number of previous settlers in a habitat and the subsequent behavior of new arrivals at that habitat. Clearings containing the types of microhabitat preferred by juveniles were established in the field, several juvenile residents were allowed to establish territories in enclosures in the center of each clearing, and then naturally occurring immigrants were allowed access to the empty microhabitat surrounding the enclosures. Arrival rates and the probability of settlement were monitored on a daily basis from the day the first juveniles arrived until several days after the last juvenile had settled (= saturation). In each of seven trials, arrival rates were comparable early and late in the settlement process, and were unrelated to the degree of habitat saturation. Arrival rates did vary on a temporal basis, probably as a result of environmental factors affecting egg laying and hatching schedules, and habitats with high arrival rates saturated more quickly than those with lower arrival rates. All of the individuals arriving at the clearings did not settle, but settlers and non-settlers did not differ with respect to competitive ability, as measured by body size. The probability of settlement increased as settlement proceeded in each of seven trials, up to the day of saturation. These results refute the commonly held assumptions that prospective territory owners avoid entering relatively full habitats, and that they prefer to settle in relatively unsaturated habitats. The discussion considers why assumptions about the behavioral processes of habitat selection are so widely accepted, given the dearth of empirical information on the subject.

Introduction

Although habitat selection is thought to have important effects on ecology and evolution (Cody 1985; Wiens 1985; symposium in Evolutionary Ecology, 1987, vol 1,

no 4), we know surprisingly little about the proximate bases of this behavior in free-living animals. In the absence of empirical data, theoreticians often rely on assumptions about the proximate behavioral mechanisms involved in habitat choice. For instance, many authors have assumed that prospective settlers in territorial species would avoid patches of habitat that already contain a high density of previous settlers, and have incorporated this assumption into their theoretical or empirical studies (Kluyver and Tinbergen 1953; Fretwell and Lucas 1970; Fretwell 1972; Krebs 1977). However, some field studies indicate that newcomers may prefer to settle next to established territory owners, rather than taking equivalent, isolated territories within the same patch of habitat (review in Stamps 1988, see also Stamps and Krishnan 1990, Smith and Peacock in press). By extension, the behavioral processes responsible for the formation of territorial aggregations within a patch of habitat might also encourage prospective settlers to settle in patches containing established residents, rather than in comparable patches containing few territory owners (e.g. Orians 1961; Shields et al. 1988; Stamps 1988; Smith and Peacock in press). Hence, there are two diametrically opposing hypothesis about the possible effects of conspecifics on habitat selection in territorial species. The 'avoidance' hypothesis predicts that newcomers would be more apt to settle in relatively empty than in relatively full patches of habitat, whereas the 'attraction' hypothesis predicts the opposite relationship between settlement and the number of previous residents a patch.

One way to test the 'avoidance' and 'attraction' hypotheses is to study a species in which newcomers arrive sequentially at a patch of territorial habitat (e.g. sequential settlement, sensu van den Assem 1967). The 'avoidance' hypothesis predicts that the rate of settlement should be highest when the patch is relatively empty. As the patch gradually fills, settlement rates are expected to decline, and as the patch becomes saturated, settlement rates should approach zero. Conversely, the 'attraction' hypothesis predicts that the rate of settlement should be relatively low for an empty patch, increase

as the patch acquires territorial residents, and then abruptly drop to zero when the patch becomes saturated. In other words, from the day the first individual arrives at a patch until the day that the last individual settles there, the 'avoidance' hypothesis predicts a decline in settlement rates, while the reverse is true for the 'attraction' hypothesis.

Settlement rate is in turn a function of two other variables: the rate at which newcomers arrive at a particular patch, and the probability that they will settle after entering the patch. Depending on the species and the situation, conspecifics could affect the settlement process by influencing either of these variables (see also Smith and Peacock, in press). For instance, if territory owners advertise their presence by visual, auditory, or other signals perceptible from outside of the patch boundaries, then newcomers might not have to enter a particular patch in order to assess the number of territory owners already residing there (Kluyver and Tinbergen 1953; Krebs 1977; Stamps 1988; Smith and Peacock in press). In this situation, the presence or number of previous settlers within a patch might affect the tendency of newcomers to enter that patch. Conversely, new arrivals might need to interact with established residents before deciding whether or not to settle in a particular patch. In that case, the presence or number of previous settlers might have little effect on arrival rates, but instead affect the propensity of new arrivals to settle after investigating the patch. Hence, conspecific avoidance or conspecific attraction could affect habitat selection in either of two ways, by changing arrival rates, or by changing the probability of settlement.

Juvenile lizards (*Anolis aeneus*) were used to test these and related assumptions and hypotheses about the relationship between habitat saturation and habitat selection behavior. These lizards hatch in woodland habitats from eggs laid one at a time over a long breeding season (July to December, Stamps 1975; Stamps and Crews 1976). Soon after hatching at about 20 mm snout-vent length, juveniles travel to clearings, in which they settle and defend small feeding territories (Stamps 1978, 1983a, b). Territory owners have a strong prior residency advantage over new hatchlings arriving at clearings (Stamps 1983b, 1987a), and residents almost never lose their territories to new arrivals. Rates of survival are very high for clearing residents, and most juveniles remain on their territories until they reach a subadult size of about 30 mm and then emigrate from the clearing back into the woodland (Stamps and Tollestrup 1984). As a result of this ontogenetic shift in habitat preferences, juvenile territorial neighborhoods are spatially segregated from the microhabitats used by subadults and adults of the same species.

The natural history of this species is ideal for studying the relationship between conspecifics and habitat selection in free-living territorial animals. Since the microhabitats preferred by juveniles are not used by larger members of the same species, new arrivals are similar in size and competitive ability to established territory owners within the same patch. Potential settlers (newly hatched juveniles) emerge over a long breeding season,

so that early and late arrivals into the same clearing are comparable with respect to age, size, and other factors that might affect their settlement behavior. Finally, prospective settlers are expected to have had comparable experiences prior to entering a given clearing; in particular, none of them would have prior experience with either that clearing or its inhabitants. Hence, in *Anolis aeneus*, the relationship between settlement behavior and an individual's date of arrival can be studied in the absence of many of the factors that might confound a similar study in other species.

In contrast, in other territorial species latecomers may differ considerably in size, competitive ability, resource requirements and other attributes from earlier settlers in the same habitat. For example, tiny larval fish settle on reefs that already contain much larger adults of the same species (Sweatman 1985), while in many migratory birds, young prospective owners arrive after older individuals have already established their territories (review in Hill 1989). An additional complication in many migratory species is the phenomenon of site tenacity, in which territory owners return to the same habitats and territories they used in previous years (Beletsky and Orians 1989; Schieck and Hannon 1989). Site tenacity implies that in any given season, all new arrivals are not equivalent with respect to their prior experience with a given patch and its inhabitants. Hence, in many territorial species, relationship between arrival date and settlement behavior may be confounded by relationships between arrival dates and a variety of other ecological and behavioral factors.

Methods

Juvenile *Anolis aeneus* were studied from July 19 to September 11, 1986 in thorn-scrub *Acacia* habitat near Grand Anse, Grenada, in the West Indies. The site and general methods have been discussed in previous publications (Stamps 1983a, b, 1984a, b, 1987a, 1988). Three small clearings (20, 32 and 40 m²) were cut into the woodland, leaving the small plants and twigs preferred by juveniles. Extra twigs and plastic leaves were added, and arranged in the configurations preferred by juveniles, forming a set of "homesites" suitable for juvenile settlement (see also Stamps and Tollustrup 1984). Prior to each trial, any juveniles in the clearing or at the periphery of the clearing were removed. Juvenile *Anolis aeneus* are reluctant to settle in totally empty clearings, so to expedite the settlement process, four juvenile *Anolis aeneus* were placed in suitable habitat within clear-walled enclosures measuring 1.23 m by 2.46 m by 0.45 m in the center of each clearing. Juveniles living in these types of enclosures interact with juveniles outside using the standard assortment of visual displays (Stamps 1987b).

Each clearing was visited one to 3 times each day (depending upon the weather) between the hours of 0630–1100 and 1530–1730, during which time the entire clearing was carefully searched for juveniles (see also Stamps 1988). Juveniles observed in the clearing for the first time were captured, toe-clipped and color-marked and then replaced on their original perch; this procedure required less than 5 min. The locations of all previously marked juveniles within the clearings were noted on each visit.

Day 1 was the day on which the first juvenile arrived in the clearing; this and any subsequent juveniles observed in the clearing were termed 'arrivals'. Juveniles were considered to be 'settlers' if they remained in the clearing for more than 48 h; all of the settlers remained in the clearing until the end of their respective

Table 1. Results of settlement experiments

Clearing	Trial No.	Dates	X̄ no. arrivals/day[b]	Total no. of arrivals[a]	Days to saturation	Final number of settlers	Probability of settlement[b]
A	1	20 July–8 Aug.	1.00	20	15	6	0.40
B	2	26 July–12 Aug.	1.00	17	13	6	0.46
A	3	10 Aug.–20 Aug.	1.67	16	9	6	0.40
B	4	16 Aug.–26 Aug.	2.00	17	4	4	0.50
C	5	21 Aug.–30 Aug.	2.80	18	5	8	0.57
B	6	29 Aug.–11 Sept.	1.33	16	12	4	0.25
C	7	1 Sept.–11 Sept.	1.71	13	7	7	0.58

[a] Includes pre and post-saturation period
[b] Presaturation period only

trials. Three criteria were used for terminating trials: 1) all of the homesites within the clearing had been claimed by a settler, 2) at least 5 days had elapsed after the last settler had arrived, and/or 3) at least 4 arrivals appeared in the clearing but did not settle. Criterion #1 was used to terminate 2 trials, criteria #2 and #3 were used for 1 trial each, and in the remaining 3 trials, both criteria #2 and #3 applied. At the end of each trial all of the juveniles in the clearing were removed, including those inside the enclosure.

Arrivals that disappeared from the clearing within 48 h were considered to have emigrated, not died. Mortality rates are very low for juveniles that live in clearings (Stamps 1983b, Stamps and Tollestrup 1984), and in the current study, the activity of the human observers discouraged visits by most of the predators capable of capturing juveniles in clearings (e.g. Carib grackles, *Quiscalus lugubris*, Stamps 1983a). Long-term behavioral observations also suggest that *Anolis aeneus* juveniles sample and then emigrate from potential habitats. For instance, I have frequently observed new hatchlings run into clearings, spend several hours to a day exploring vacant homesites there, and then jump into the dense underbrush at the clearing edge, never to be seen again (Stamps, unpublished data). Unfortunately, juveniles disappear into tangles of vegetation when moving through woodland habitats, so it was not practical to try and locate emigrants in the areas surrounding the experimental clearings.

In all, 7 trials were run in three different clearings during the 2 month period (Table 1). The number of new juveniles arriving at each clearing was calculated for each day of the study. Frequently, 2 clearings were observed on the same day (see schedule in Table 1); in those cases, the arrival rate for that day represents the average for both clearings. Seasonal changes in arrival rates were studied by dividing the entire study period into 7 periods of 7 days each, and calculating the average arrival rate per day for each of these weekly periods. Whenever a particular clearing was observed for at least 4 successive days within 1 of the weekly periods, I also calculated the average arrival rate per day for that clearing. These data were used to determine if different clearings covaried with respect to seasonal changes in arrival rates.

Rainfall is correlated with food levels and growth rates for juvenile *Anolis aeneus* (review in Stamps and Eason 1989), so rainfall was recorded each day during the study.

Parametric statistical tests were inappropriate for many of the analyses in this paper, e.g. because samples were small and not normally distributed, or because unequal variances across trials precluded the use of Anova. Hence, with the exceptions noted below, nonparametric analyses were used in the current study.

Results

Juveniles arriving at clearings

On average, 1.40 (SE = ±0.15) juveniles arrived per day per clearing over the two month observation period. Ac-

ross all 3 clearings, the average number of arrivals per day gradually increased from week 1 to 6 and then declined (Fig. 1). This same pattern was also evident when average arrival rates were calculated for individual clearings in successive weeks (Fig. 1).

Juvenile arrival rates did not seem to be related to short-term fluctuations in environmental factors such as rainfall. The average number of juveniles arriving per clearing per day was not significantly related to the amount of rainfall on the same day, nor to the amount of rainfall on any of 7 previous days (cross-correlations, highest correlation $r_s = 0.22$, $N = 59$ days). If other environmental factors such as wind, cloud cover, temperature, and so forth had affected arrival rates, different
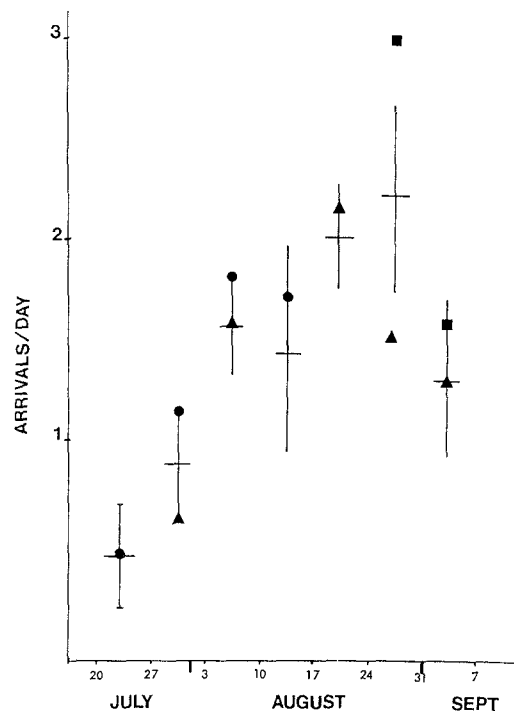

Fig. 1. The average number of arrivals per clearing per day (±SE) for each of 7 weekly periods of the study. *Bars* and *lines* are based upon data from all of the clearings observed during each weekly period, symbols represent the average arrival rates for individual clearings that were sampled for at least 4 successive days during each weekly period (clearing A = *circles*, clearing B = *triangles*, and clearing C = *squares*; see also methods)
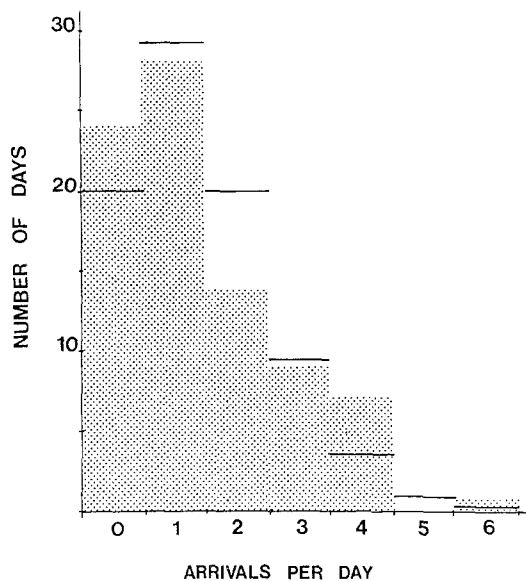
Fig. 2. Stippled: the number of new arrivals per day per clearing, combined data from the entire study. *Bars:* the predicted number of arrivals per day, based upon a Poisson distribution with a mean = 1.4 arrivals per day

clearings sampled on the same dates should show synchronous fluctuations in arrival rates. However, there was no relationship between the number of juveniles arriving at 2 different clearings on the same days ($N = 31$ days, $r_s = 0.05$).

There was no indication that juvenile arrival rates were related to the degree of saturation of the habitat. 3 trials had positive relationships between date and the number of arrivals per day, 4 had negative relationships; the average Spearman correlation coefficient for the seven trials, $r_s = 0.08$ (SD = 0.29). Similarly, if juveniles were able to assess the degree of saturation from outside of a clearing, arrival rates at any given clearing should have been higher prior to than following saturation. In fact, arrival rates were higher following saturation than before in 2 trials, equal in one trial, and lower in 4 trials. These results do not support the hypothesis that juvenile entry into clearings is influenced by the number of conspecifics already residing there.

Over the entire experiment, the number of arrivals per day per clearing fit a poisson distribution with a mean of 1.40 ($X^2 = 3.2$, $P = 0.20$, Fig. 2). This suggests that juveniles enter clearings independently of one another (e.g. they neither entered clearings together, nor did they avoid entering clearings if another hatchling was doing so).

Settlement

The number of days required for saturation varied from 4 to 15 days in the seven trials (Table 1). This variance did not appear to be related to differences in habitat quality. For example, if some clearings were of higher quality than others, one might expect to see consistent differences among clearings in saturation times. How-

ever, there was as much variation within as among clearings in the number of days required for saturation (Table 1).

Another factor that might affect time to saturation is the arrival rate of juveniles during the colonization period. Given the seasonal variation in arrival rates (see above), clearings might saturate more rapidly when arrival rates were high than when they were lower. In fact, there was a strong negative relationship between the number of days required for saturation and the average number of arrivals per day prior to saturation, $r_s = -0.97$, $p < 0.01$, Table 1). The same inverse relationship between days to saturation and arrival rate prior to saturation was obvious within individual clearings (e.g. clearing B, Table 1). These results suggest that the period required for settlement to saturation was primarily a function of the rate at which potential settlers arrived at the habitat.

Even during the presaturation period, not all of the new arrivals entering clearings settled there. For the period from day 1 to the day of saturation, the proportion of new arrivals that eventually settled ranged from 25% to 58% across the 7 trials (Table 1). The number of replicates per clearing was insufficient to determine whether settlement success varied consistently among the 3 clearings.

There was no indication that settlers were more competitive than were nonsettlers in the same trials. In this species, success in aggressive encounters is size-related, given that both individuals have had the same amount of prior experience with a habitat or a territory (Stamps and Eason 1989). However, body size was unrelated to the probability of settlement for juveniles arriving during the presaturation period. The snout-vent lengths of new arrivals were normally distributed and both average length and variance in length were equivalent across trials, so parametric analysis were appropriate for analyzing this variable. Overall, there was no difference in the average sizes or standard deviations in sizes of arrivals that settled versus those that did not settle (settlers: 20.8 ± 0.90 mm, $N = 41$; nonsettlers: 20.5 ± 0.92 mm, $N = 50$). The same result was apparent within trials (two-way Anova with trial and settlement status as factors: trial, $F = 0.45$, $p = 0.85$, n.s.; settlement status, $F = 1.96$, $P = 0.17$, n.s.; $N = 91$ juveniles).

Juveniles arriving together at a habitat might have a higher probability of settling, because territory owners seem to have difficulty expelling several simultaneous intruders (Stamps 1990). In that case, we might expect a positive relationship between the number of juveniles arriving at a clearing on a given day and the percent of those juveniles that eventually settled. However, there was little evidence of such a relationship ($r_s = 0.06$, $N = 41$ days).

Since all juveniles arriving at clearings did not settle, it was possible to study the relationship between the probability of settlement and the degree of habitat saturation (see Introduction). For each day of the presaturation period, new arrivals were scored as to whether or not they eventually settled in the clearing. These data were used to compute the probability of settlement for

each day on which at least 1 juvenile arrived at the clearing.

The results of this analysis supported the 'attraction' hypothesis: early arrivals were less apt to settle than were latecomers into the same clearings. In all 7 trials, the proportion of new arrivals that settled increased as a function of time from day 1 to the day of saturation (Sign test, $P = 0.008$, one-tailed). On average, only 24% of the new arrivals that appeared on day 1 settled, versus an average 58% settlement success for those juveniles that arrived from day 2 up to the day of saturation. In all 7 trials, the proportion of juveniles that settled was lower for juveniles arriving on the first day than for those that arrived later during the pre-saturation period (Sign test, $P = 0.008$, one-tailed).

Looking at it another way, the probability of settlement increased as a function of the number of previous settlers in the same patch of habitat. For each trial, I calculated the number of settlers present for each day on which at least one new arrival appeared in the clearing. In all 7 trials the probability of settlement increased as a function of the number of juveniles already residing in the clearing (Sign test, $P = 0.008$, one-tailed). Hence, the presence of conspecific settlers seemed to encourage, rather than to discourage, settlement by later arrivals into the same habitat.

Discussion

A first step in habitat selection is the decision whether or not to enter a particular habitat. In juvenile *Anolis aeneus*, this decision was not contingent upon the degree of saturation of the habitat. Arrival rates neither declined nor increased as settlement proceeded, nor were arrival rates lower after saturation than they were prior to saturation. Hence, this study did not support the assumption that prospective settlers would avoid searching for territories in saturated habitats.

This result might be due to the high costs of assessing conspecific densities prior to entering a habitat. Juveniles traveling through woodland habitats or perched at the edge of clearings are vulnerable to predation, because these areas harbor a high density of the sit-and-wait saurian predators that eat juvenile *Anolis aeneus* (Stamps 1983a). Conversely, locating conspecifics and territorial vacancies by visual inspection would take a minimum of several hours to a day or more. Juveniles display and move relatively infrequently, and juvenile microhabitats within clearings often contain many visual obstacles, so that many of the residents are out of sight a large portion of the time. Hence, newcomers poised at the edge of a clearing are in a dangerous location, and they would have to remain in that location for a long period in order to accurately estimate the number and position of conspecific residents in the clearing. Under the circumstances, it is not surprising that hatchlings dash into clearings without regard to the number of other individuals already living there.

This argument suggests that high costs of long-range assessment might discourage potential settlers from trying to estimate densities prior to entering prospective habitats. However, arrival rates might still be negatively related to settler densities for those species in which long-distance assessment of habitat saturation was more feasible. Birds would seem to be likely candidates for assessment prior to entry, because of the conspicuous visual and vocal displays of territorial residents. However, I was unable to find any studies which have quantified the arrival rates of prospective avian settlers as a function of the degree of habitat saturation. Yasukawa and Searcy (1985) looked at a related question: the relationship between the density of established territory owners and intrusion rates during the post-settlement period. They were surprised to find a positive, not a negative, relationship between the intrusion per unit area and male density in red-winged blackbirds, even after they statistically controlled for the effects of territory quality. In addition, they were unable to find any cases in the literature showing a negative relationship between conspecific density and intruder rates. Hence, the assumption that prospective avian settlers would tend to avoid relatively saturated habitats has not yet been validated.

Across the clearings and the trials, juvenile *Anolis aeneus* arrival rates varied on a temporal, but not a spatial basis. The lack of appreciable differences in arrival rates across clearings was comforting, since all of the clearings were initially designed to be highly attractive to juveniles. In addition, all of the clearings were embedded in the same woodland habitat, so that the source of potential settlers (i.e. the density of egg-laying females in adjacent habitats) was comparable for the three clearings. It is likely that under natural conditions, both the quality of the territorial patch and the nature of the surrounding habitat would affect the number of hatchlings arriving at clearings (see also Stamps 1990).

The seasonal variation in arrival rates observed in this study was probably a function of fluctuations in female egg laying schedules and egg survival. Female *Anolis aeneus* tend to lay eggs after heavy rainfall, and retain eggs during dry periods, so the first heavy rain after a dry period leads to relatively synchronous egg laying among the females in a given habitat (Stamps 1976). In addition, long droughts may desiccate buried eggs, resulting in a dearth of hatchlings in subsequent weeks (Andrews 1988; Stamps, unpubl. data). Thus, there is usually a gradual increase in hatchlings from mid July to mid September (reflecting the beginning of egg laying at the onset of the rainy season a month earlier), and within the 6 month rainy season the numbers of new hatchlings may fluctuate as a result of rainfall patterns in previous months.

This discussion of *Anolis* natural history highlights the fact that factors extrinsic to the quality of a particular habitat may have important effects on the rates at which potential settlers arrive at that habitat (for other examples see Pulliam 1988; Stamps 1990). To the extent that arrival rates vary for reasons unrelated to the quality of a particular patch of territorial habitat, it would be a mistake to assume that habitats attracting more potential settlers were *necessarily* of higher quality than those attracting fewer settlers. Similarly, the results of

this study suggests that arrival rates were inversely related to the time required for saturation, such that patches of habitat with high arrival rates filled more quickly than those with lower arrival rates. Again, to the extent that arrival rates are independent of patch quality, it would be dangerous to assume that high quality habitats would necessarily saturate more rapidly than low quality habitats. Assumptions about relationships between habitat quality and filling rates have appeared in several theoretical models of habitat selection (e.g. Brown 1969; Fretwell and Lucas 1970), but so far the empirical data on this question are sparse and indirect (O'Connor and Fuller 1985).

After prospective settlers enter a habitat, a second important decision is whether or not to settle in that habitat. Conspecifics may affect this decision in a variety of ways. First, the probability of settlement may be affected by the presence or absence of conspecifics. The current experimental design sidestepped this question by "seeding" each clearing with juveniles within plastic-walled enclosures. This was done because previous studied suggested that juvenile *Anolis aeneus* might be reluctant to settle in empty clearings. That is, previous studies indicated that the presence of conspecifics might increase the probability of settlement in this species. Future plans call for an explicit test of this assumption, with an emphasis on the characteristics of those individuals who are the "pioneers" in totally empty habitats.

The probability of settlement may also be affected by the number of conspecifics already residing within a particular habitat. In the current study, the probability of settling increased as the settlement process proceeded, and newcomers entering nearly empty habitats were less likely to settle than those entering the same habitats later during the settlement sequence. These results refute the commonly held assumption that potential settlers would be more apt to settle in relatively unsaturated habitats, and suggest instead that these lizard hatchlings prefer to settle in reasonably full territorial neighborhoods.

I was unable to find comparable data on the effects of conspecifics on settlement for any other territorial vertebrate. The closest analogies to the current study are found in the literature on sessile invertebrates, in which larvae are more apt to settle in the presence of other newly settled individuals, and in which new settlers tend to space themselves at some distance from previous arrivals (e.g. Crisp 1961; Buss 1981). Other studies of fish and invertebrates suggest that larvae may preferentially settle in areas used by conspecific adults (e.g. Crisp 1984; Sweatman 1985, 1988; Woodin 1986; Raimondi 1988; also see the Introduction), but in such cases the new arrivals are much smaller than the previous residents in the same habitat.

'Habitat saturation' is difficult to define in this situation, because the resource requirements and competitive abilities of the tiny newcomers and the larger conspecific residents are quite different. Indeed, several studies indicate that the response of larvae to settled conspecifics may vary, depending upon the size of those residents. For instance, Crisp (1961) found that larval barnacles settled on top of larger conspecifics, but settled at a particular distance from newly-settled conspecifics of the same size as themselves. Similarly, Buss (1981) found a positive correlation between the density of small bryozoans and the probability that conspecific larvae would settle, but this correlation disappeared when the attached bryozoans were much larger than the newcomers.

Given the lack of empirical information on the effects of the density of competitors on settlement in territorial species, it is worth asking why so many people have been so quick to assume that prospective territory owners would tend to prefer relatively empty habitats. One possible reason is that assumptions about proximate behavioral mechanisms are often predicated upon other implicit assumptions about behavior. In the case of habitat selection, if one assumes 1) that fitness decreases as density increases, and 2) that animals can accurately measure both habitat quality and the density of conspecifics, then it makes intuitive sense that prospective owners would be more apt to settle in habitats with relatively low densities than in comparable, more saturated habitats. Both assumptions 1) and 2) were incorporated into some of the early discussions of habitat selection (Lack 1966; Brown 1969a; Fretwell and Lucas 1970; Fretwell 1972), and they have tended to permeate the literature ever since (e.g. Partridge 1978; Whitham 1980; O'Connor and Fuller 1985; Rosenzweig 1985; Morris 1989).

In contrast, early work by Allee and others suggested that territorial animals might benefit from having neighbors, in which case fitness would first increase as a function of density, and then (perhaps) decline again at very high densities (Lack 1948; Allee et al. 1949; Allee 1951; Fisher 1954; van den Assem 1967). This theme has reemerged in recent years, as workers have begun to reconsider the potential benefits of living in colonies (Buss 1981; Wethey 1984; Shields et al. 1988) or territorial neighborhoods (Getty 1987; Stamps 1988; Beletsky and Orians 1989). Other workers have pointed out that animals may be unable to accurately assess either habitat quality or population density when they choose a habitat (Hildén 1965; Brown 1969b; Seastedt and MacLean 1979; Partridge 1978; Stamps 1987b; 1990).

Of course, if one assumes that living in a tight-knit territorial neighborhood has a positive effect on fitness, then it follows that new arrivals should prefer a patch of habitat containing many potential neighbors to a comparable patch of habitat with only a few residents. Similarly, the assumption that potential settlers have difficulty in assessing habitat quality suggests that newcomers might use the presence and density of conspecifics as a cue to habitat quality, again preferring to settle in patches that already contain established residents.

Hence, assumptions about how a territorial animal should respond to conspecifics while settling depend a great deal upon assumptions about other behavioral questions, such as the type of proximal behavioral rules used for habitat assessment or the form of the relationship between population density and important components of fitness. Since these underlying assumptions are rarely tested, it may be dangerous to use them to predict

how new arrivals should respond to the presence or density of previous settlers in a particular habitat.

On a more positive note, the important role of habitat selection in ecology, evolution and conservation biology, coupled with our relative ignorance about the proximate bases and fitness consequences of habitat selection behavior, suggests that this would be a fruitful area for future research. For example, applied problems in conservation biology often hinge on problems of habitat selection, such as how to attract new settlers to an empty reserve, or how to transfer residents from a deteriorating or disappearing habitat to a higher quality, protected habitat. The practical goal of these projects is to induce animals to settle where humans want them to settle, but given the lack of information on the cues that induce territorial settlement under natural conditions, such attempts frequently meet with failure (Griffith et al. 1989). The relationship between the probability of settlement and habitat density is particularly germane to this question. For instance, if the probability of settlement is negatively related to the number of conspecifics in the habitat, then one should release prospective settlers evenly and sparsely across the new habitat. However, if these two variables are positively related, then one might use behavioral decoys, tape recordings of territorial advertisement signals, or other techniques to convince newcomers that a habitat already contains a group of satisfied territory owners (see also Smith and Peacock in press). Hence, a number of important theoretical and practical problems in other fields may depend on further studies of the proximate behavioral bases of habitat selection.

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