



Mechanisms for the formation and maintenance of traditional night roost aggregations in a territorial damselfly

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(Received 6 April 1999; initial acceptance 6 August 1999;
final acceptance 28 April 2000; MS. number: A8460)

Communal roosting has been studied extensively in birds, but the mechanisms and functions of this taxonomically widespread behaviour pattern remain poorly understood. We studied the roosting behaviour of rubyspot damselflies, *Hetaerina americana*, in relation to sex and territorial status, and conducted field experiments to test for specific mechanisms of roost formation and maintenance. Both sexes tended to return close to their previous night's roost, but only males were significantly more roost site faithful than chance expectations based on individual day ranges. Males were more roost site faithful when they held mating territories. After acquiring a territory, males usually began roosting closer to the territory after a delay of a few days. Roosts were not located at sites that reduced the daily commuting distance between hunting areas and territories; males generally hunted closer to their territories than to their roosts. In field experiments, sites 'seeded' with synthetic models of male rubyspots attracted more recruits than vacant control sites and control sites seeded with nonrubyspot (clear-winged) damselfly models. Sites seeded repeatedly with rubyspot models often remained popular for roosting after the models were removed, suggesting that the models established new traditional roosts. These results indicate that conspecific attraction and individual spatial memory together may be sufficient to explain, at a proximate level, the traditional night roost aggregations of this species. We discuss these results in relation to functional hypotheses for roost site choice and fidelity.

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Roosting aggregations have been observed in flatworms, arthropods and vertebrates (Wynne-Edwards 1962; Reynierse et al. 1969; Eiserer 1984; Vulinec 1990), and have been the focus of hundreds of studies. In many species, the location of roosting aggregations appears traditional; aggregations appear at the same sites from day to day, and sometimes year to year, even though other suitable locations seem available (Rau & Rau 1916; Jones 1930; Wynne-Edwards 1962; Eiserer 1984; Prentice & Walker 1991). Many authors have discussed the possible mechanisms and functions of such aggregations (e.g. Fleming 1981; DeVries et al. 1987; Perlmutter 1992; Doucette & Reeb 1994; Danchin & Richner, in press; Marzluff & Heinrich, in press), but studies of the long-term patterns of roosting behaviour of marked individuals are rare. Relatively little is known about roost site choice, the causes of roost site shifts, or the mechanisms responsible for the development and maintenance of

spatially stable roosting aggregations. Such data are crucial for testing individual-based models of how and why roost aggregations form (e.g. Ward & Zahavi 1973; Weatherhead 1983; Caccamise & Morrison 1986; Richner & Heeb 1996).

Our understanding of roosting behaviour is hampered, in part, by the difficulty in tracking individual animals and of conducting field experiments with replication on an appropriate scale. It is necessary not only to track the roosting sites of individuals over time but also to follow changes in other relevant locations, such as foraging areas and territories. Recent radio-tracking studies have provided such data for bats, birds and snails (e.g. Heisterberg et al. 1984; Bailey 1989; Giroux 1991; Lewis 1995; King 1996; Marzluff et al. 1996), but the logistics and expense of radio tracking can lead to small sample sizes of both individuals and roosts. For taxa that do not lend themselves to radio tracking (e.g. insects), researchers are limited by the number of roosting aggregations they can find and the spatial distribution of the aggregations (e.g. DeVries et al. 1987; Miller 1989). Controlled field experiments, with replication of the treatments, are required to test possible mechanisms

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of roost site formation and maintenance, but such experiments are difficult to perform on most species.

The rubyspot damselfly, *Hetaerina americana*, is an unusually tractable species for studying roosting behaviour. Roosts, mating territories and foraging areas all occur along streams; the spatial scale is such that it is feasible to study multiple roosts simultaneously and to follow changes in roost site usage over time. Both sexes are easy to find and have limited movement; hundreds of individuals can be marked and followed among roosts over their relatively short lives (Grether 1996a, b). Elsewhere we present a quantitative analysis of the spatial and temporal patterns of roost site use in this species, in relation to features of the habitat, air temperature and population density (Switzer & Grether 2000).

In this paper, we present individual level analyses of roosting behaviour and the results of experiments designed to probe the mechanisms of roost formation and maintenance. More specifically, we examine how the roost site fidelity of individual damselflies varies in relation to sex and territorial status, how the acquisition of a mating territory affects where males roost, and where the roosting sites, territories and hunting areas of individual males are located in relation to each other. Our experiments test for two proximate mechanisms of roost formation and maintenance: conspecific attraction and individual spatial memory. Based on the results, we develop a conceptual model of the roosting process. The results also shorten the list of possible functions of communal roosting in this species (see below).

Study Species

Here we review pertinent details of rubyspot natural history, as observed at our study site in the Coastal Range Mountains of California and described in more detail by Switzer & Grether (2000).

During the warm hours of the day, males compete to defend small (1–4 m²) mating territories along stream riffles (Grether 1996b). Once a male acquires a territory, he returns to defend the same site each morning until death or forceful eviction (Grether 1996b). Males rarely hunt on their territories; most hunting occurs away from territories along pools of slow-moving water, from the west bank of the stream in the morning and from the east bank in the late afternoon (Grether & Grey 1996). In the late afternoon, males leave their territories and both sexes hunt by launching attacks at small flying insects from perches along the stream bank (Grether & Grey 1996). Around dusk, both sexes settle into roosts in the bank vegetation, solitarily or in groups (Switzer & Grether 2000). After sunrise, the animals disperse from the roosts and resume hunting nearby (Grether & Grey 1996). In the late morning, males begin competing for territories, and the diurnal cycle repeats.

During the summer, rubyspots roost exclusively on vegetation and primarily on the emergent portions of living streamside plants, usually 0.2–2 m above the ground or water, within 0.5 m of the stream margin on the west bank of pools (Switzer & Grether 2000). In the spring and late autumn, roosts tend to be found further

from the stream and higher above the ground, perhaps as protection against floods (Switzer & Grether 2000). The preference for roosting on the west bank may reflect the importance to these ectotherms of being on the sunny side of the creek when the sun crests the ridge in the morning; pools may be preferred because they are the best areas for hunting. Within the streamside vegetation on the west bank of pools, roosts do not appear to be associated with particular microhabitat features. Yet, on any given night, the animals can be found clustered within these areas, sometimes in groups of up to 65 individuals (Switzer & Grether 2000). From one night to the next, some sites are consistently more popular for roosting than others; but over time, the spatial distribution of roosts changes gradually without observable changes in the habitat, suggesting that location of the roosts is partly traditional (socially learned). It is unlikely that roosting aggregations are kin aggregations, because damselflies spend most of their lives as solitary larvae (Corbet 1962), and in any case, roosting aggregation membership is quite fluid (this paper). Roosting aggregations are male biased, relative to the population sex ratio, but both sexes are found both in aggregations and solitarily (Switzer & Grether 2000).

Function of Roosting Aggregations

Several functional hypotheses for communal roosting in rubyspots can be rejected a priori. Habitat limitation cannot explain why roosting aggregations form, unless we have failed to detect the critical habitat features and these features change over time. Roosting aggregations clearly do not function as sexual rendezvous sites (Mallet 1986), because rubyspots hunt for a time before entering the roosts and again after dispersing from the roosts, and no mating occurs at the roosts. We can also rule out the thermal benefits hypotheses (Copp 1983; Eiserer 1984; Vulinec 1990), because the aggregations are loose and damselflies are ectothermic. The information centre hypothesis and related models proposed for species with patchy, unpredictable resources (reviewed in Danchin & Richner, *in press*) are unlikely to apply to rubyspots because hunting and roosting sites occur within metres of each other and in predictable locations (along pools). The aposematism hypothesis, which has been applied to explain the gregarious behaviour of other insects (Turner 1975; Copp 1983; Vulinec 1990), seems unlikely to apply to rubyspots. No damselflies are known to be noxious, toxic, or distasteful (Fincke 1994) and, although males rubyspots are conspicuously coloured, females are cryptic and both sexes are eaten by a large number of vertebrate and invertebrate species. This leaves several anti-predation hypotheses (selfish herd, Hamilton 1971; dilution, Treisman 1975; vigilance, Pulliam 1973), the safe site hypothesis (Mallett 1986), and the patch-sitting hypothesis (Caccamise & Morrison 1986).

Under the patch-sitting hypothesis, large roosting aggregations form as a result of individuals minimizing the distance between their diurnal activity centres (DACs) and supplemental feeding areas. Supplemental feeding areas are seasonably valuable food sources where

individuals feed in the morning and the evening; the animals roost communally near these sites, instead of near their respective DACs, to reduce daily commuting costs. Tests of this hypothesis remain limited to a few species of communally roosting birds (Maccarone 1987; Caccamise & Morrison 1988; Caccamise 1991; Stouffer & Caccamise 1991; Caccamise et al. 1997). Male rubyspots have discrete DACs (mating territories) and typically forage outside their territories before entering and after leaving the night roost. Thus, territorial male rubyspots fit the basic assumptions of the patch-sitting hypothesis. Here we test the model's predictions.

METHODS

Observational Study

We studied a population of rubyspots along a small perennial stream in Colusa County, California called Bear Creek (39°01'N, 122°23'W, elevation 260 m). Intensive observations were made along a straight 134-m section of Bear Creek that runs north-south and includes both pools and riffles. We marked all rubyspot damselflies in this section shortly after emergence or immigration on their left hindwing with a unique number using a black Sharpie pen. Ages were known to within 1 day or estimated using a highly reliable technique based on characters that change with age (e.g. eye darkness and wing stiffness; Grether 1996a, b). We censused roosts in the study section on 58 consecutive mornings (25 August–21 October 1991) between 0500 and 0900 hours, when the animals were inactive. During censuses, we recorded the identification number, sex and location of each rubyspot. Location data included the bank (east or west), distance along the creek with respect to marker flags (to 0.5 m), and distance from the creek (to 0.5 m). We collected day range and territoriality data continuously from the time animals left the roosts in the morning until they roosted again in the evening (see Grether 1996b for further details). We recorded hunting by rubyspots opportunistically, based on observed attacks, prey protruding from the mouth, and characteristic perching sites and postures (see Grether & Grey 1996). Based on our unpublished observations at this site in subsequent years (1992–1995), we believe that the results we report here are representative of the summer roosting behaviour of the study population.

Some individuals of both sexes repeatedly roosted at the same site. To determine whether this occurred more often than would be expected under random settlement of available roost sites, we compared observed inter-roost distances to a random expectation. Expected inter-roost distances were based on the conservative assumption that only roost sites within the up- and downstream limits of an individual's day range were available for that individual to settle. Specifically, we calculated the mean euclidian distance between the site used by an individual on one night and all sites occupied by rubyspots on the next night that were within the observed range of the individual on the intervening day. Day ranges were based on a minimum of three recorded sightings. This method

probably underestimates the inter-roost distance expected under random settlement, because day range estimates are minimum ranges based on recorded sightings, and the number of available sites probably exceeded the number actually occupied on any given night.

We compared observed inter-roost distances to two types of expected values: general and sex specific. We calculated general expected values under the assumption that all occupied sites were available for settlement by animals of both sexes. We calculated sex-specific expected values under the assumption that only sites occupied by females were available for settlement by females, and likewise for males. We restricted the analysis to individuals with two or more pairs of observed and expected inter-roost distances (282 males; 130 females), and used mean differences (expected – observed) in the analysis.

To examine the relationship between territoriality and roost site fidelity, we used the method described above to calculate observed and expected inter-roost distances for males (1) on days they held mating territories, and (2) on days they did not hold mating territories. Both types of data were available for 141 males, which enabled us to make paired within-male comparisons of observed and expected inter-roost distances to detect effects of territoriality.

As applied to territorial male rubyspots, the 'patch-sitting' hypothesis of Caccamise & Morrison (1986) predicts that males select roosts that reduce the daily commuting distance between territories and hunting areas (see Discussion). To test this prediction, we calculated roost-to-hunting area (RH) and hunting area-to-territory (HT) distances for the morning commutes of 116 males and the afternoon commutes of 34 males. Repeated measurements on a given male were averaged. The sum $RH+HT$ is a male's actual commuting distance and $2 HT$ is the round-trip distance he would have travelled had he roosted on the territory. The patch-sitting hypothesis predicts that $RH+HT$ is less than $2 HT$.

We also classified males according to which site (roost, territory, or hunting area) was usually central to (located somewhere between) the other two. For the morning commute, it was possible to classify 88 of the 116 males in this manner; the other 28 males could not be classified because, in our data set, they hunted on their territory ($N=6$) or at their roost ($N=1$), they roosted on their territory ($N=1$), their territory and hunting areas tied for central position ($N=17$), or other combinations of sites were tied for central position ($N=3$). Ties were common because of the small number of repeat observations (range 1–13 days; median 2 days). For the afternoon commute, it was possible to classify 33 of the 34 males; one male could not be classified because he hunted on his territory.

Experiments

We conducted two experiments using rubyspot models to simulate roost aggregations. The models were constructed from wire, clay, acetate, enamel paint and ink,

and were of three types. The first type, the 'rubyspot models', were painted to resemble the wing and body coloration of mature male rubyspots. The second and third type of models were developed as controls: 'clear models' had the same body size and colour as the rubyspot models but clear wings, and 'blue models' had the same body size as rubyspot models but blue bodies and clear wings.

Experiment 1: conspecific attraction

The goal of the first experiment was to determine whether conspecific attraction (of rubyspots to each other) is a plausible mechanism for roost aggregation. Rubyspot damselflies have a strong tendency to roost at the same sites night after night (Switzer & Grether 2000; also see Roost Fidelity results). Hence, to increase the probability that rubyspots would detect our models, we located the rubyspot model and control sites near natural roost aggregations. We used a paired design: one rubyspot model group and one control group for each natural aggregation ($N=33$ pairs), and three types of controls: clear models, blue models and vacant sites (no models). Groups of four models were placed at the clear and blue model sites; rubyspot model sites contained either four or eight models, to test for group size effects on recruitment. On the first morning of the experiment (18 May 1993), before the damselflies left the roosts, we marked the location of natural roost aggregations with surveyors flags. Because roosting aggregations in this species have no distinct borders, we defined an aggregation as two or more individuals within 20 cm of each other. Before the animals roosted again in the evening, we positioned one rubyspot model group and one control group 1.5 m away from and on opposite sides (up and downstream) of the flags, to ensure that reformation of natural aggregations was not confused with attraction to the models, and to control for the distance to natural aggregations. The side for the rubyspot model group was determined randomly for the first pair, and alternated thereafter. Early the next morning, we recorded the number of individuals roosting within 20 cm of the centre of the experimental and control sites. Below we refer to individuals within the criterion distance of 20 cm as 'recruits'.

Experiment 2: development and maintenance of roost sites

The main purpose of the second experiment was to determine whether new roost aggregations could be established by repeatedly 'seeding' their formation with rubyspot models. This experiment also shed light on the relative strength of conspecific attraction versus individual site memory in roost formation. On 3 August 1995, along the same reach of Bear Creek as experiment 1, we paired rubyspot six-model groups (i.e. six models/group) with vacant control sites in the vicinity of natural roost aggregations (as defined above). More natural aggregations were available during experiment 2 than during experiment 1, so we only placed models near natural aggregations of four or more individuals. Also, in contrast to experiment 1, both model and control sites were

located in the same direction from a natural aggregation (up- or downstream), at least 1.5 m from the natural aggregation and from each other. Between pairs, we varied which site was closer to a natural aggregation and whether both sites were up- or downstream. On the average, model and control sites did not differ in distance from a natural aggregation (models: 2.85 ± 0.32 m; controls: 2.90 ± 0.37 m; $N=30$ for each; Mann-Whitney U test: $U=439.5$, $P=0.87$). Individuals roosting within 20 cm of the centre of a site (which was marked with a small piece of white tape) were considered recruits for that site. We recorded the number of recruits at each site 1, 7 and 8 days after the models were originally placed. Between the roost censuses on days 7 and 8, we repositioned the models. The purpose of this manipulation was to determine whether the animals would continue roosting at sites 'seeded' with models even after the models were removed. With half of the model-control site pairs, we moved the rubyspot models to the control site, turning the former control site into a model site and the former model site into a control site. With the other half of the model-control site pairs, we removed and then replaced the models at the same site, as a sham manipulation. These two manipulations were alternated down the stream. Analyses are based on the difference in the number of individuals recruited to a site before versus after the manipulation.

Statistical Procedures

Data were transformed to meet assumptions of the statistical tests as needed. Day range and observed and expected inter-roost distances were $\ln(x+0.01)$ -transformed; roost-to-territory distances were square-root transformed. Nonparametric statistics were corrected for ties. The P values we report are two tailed.

RESULTS

Observational Study

Roost fidelity

Individuals roosted within 0.5 m of their previous night's roost 17% of the time, within 1 m 33% of the time, and within 2 m 54% of the time (Fig. 1). To determine whether this degree of roost site fidelity could have arisen through random settlement of available roosts, we compared the observed inter-roost distance of individuals to random expectations based on individual day ranges (see Methods). The inter-roost distances of males were smaller than expected under random settlement (Wilcoxon test comparing mean expected-observed inter-roost distances to zero: general: $Z=5.26$, $N=282$, $P<0.0001$; sex specific: $Z=6.23$, $N=282$, $P<0.0001$), but those of females were not (general $Z=0.18$, $N=130$, $P=0.86$; sex specific: $Z=0.12$, $N=130$, $P=0.90$). Females did not have greater inter-roost distances than males (Mann-Whitney U test: $Z=1.32$, $N_f=130$, $N_m=282$, $P=0.18$), but females had smaller day ranges ($Z=7.26$, $P<0.0001$) and smaller expected inter-roost distances

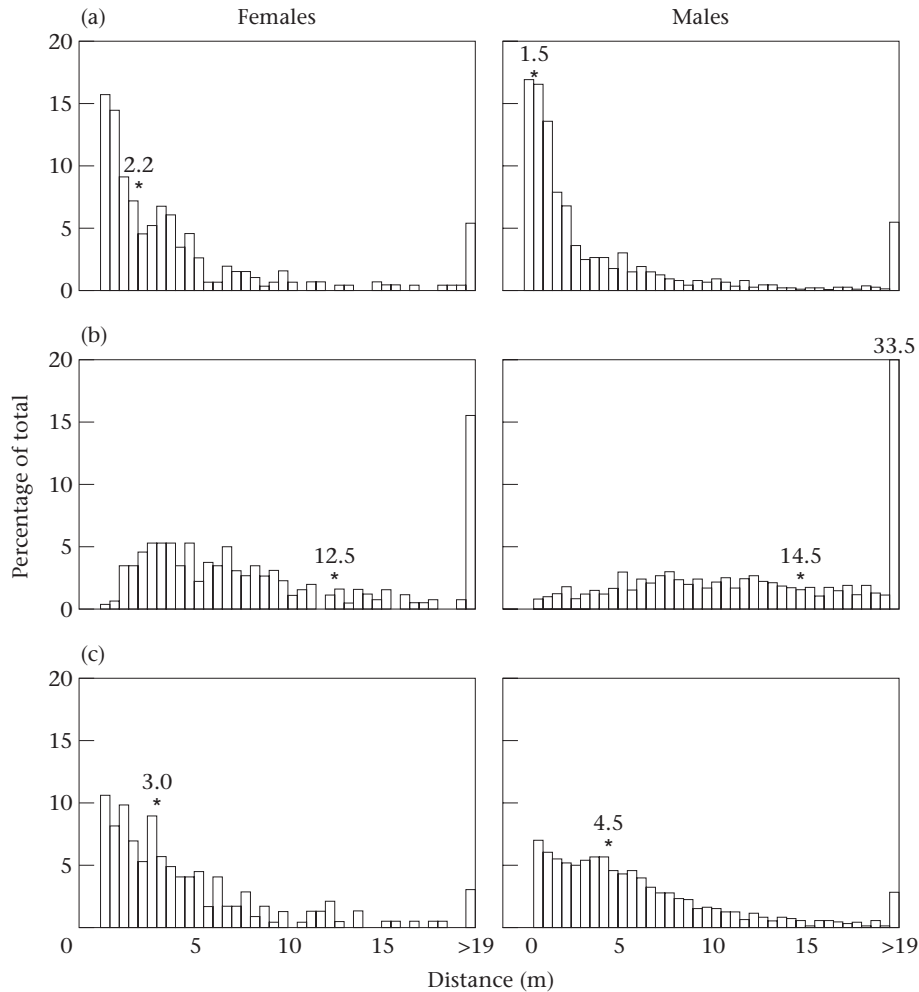


Figure 1. (a) Observed distances between the roosts used by individual damselflies on consecutive nights. (b) Observed day ranges. (c) Expected inter-roost distances based on the availability of roosts within an individual's day range. Repeat measurements on individuals with two or more observed inter-roost distances are pooled here (262 measurements on 130 females, 1826 measurements on 282 males). The median of each distribution is indicated with an asterisk and the median is given above the asterisk. See text for further details and the unpooled statistical analysis of individual means.

than males (general: $Z=5.07$, $P<0.0001$; sex specific: $Z=4.02$, $P<0.0001$). Consequently, the difference between expected and observed inter-roost distances was greater for males than for females (general: $Z=3.36$, $P=0.0008$; sex specific: $Z=3.99$, $P<0.0001$). Thus, males showed greater roost site fidelity than females relative to their respective day ranges but not on an absolute distance basis.

When males held daytime mating territories, they had smaller inter-roost distances, smaller day ranges, and smaller expected inter-roost distances than when they did not hold territories (Wilcoxon signed-ranks test: day range: $Z=4.96$, $N=141$, $P<0.0001$; inter-roost distance: $Z=3.70$, $N=141$, $P=0.0002$; expected inter-roost distance: $Z=4.61$, $N=141$, $P<0.0001$). These results were not confounded with age, because the mean age of males in this sample was not correlated with territorial status (non-territorial age: 20.97 ± 0.82 days; territorial age: 20.08 ± 0.41 days; paired t test: $t_{140}=0.89$, $P=0.22$). The difference between expected and observed inter-roost distances was

not significantly affected by a male's territorial status (Wilcoxon matched-pairs signed-ranks test: $Z=0.59$, $N=141$, $P=0.55$). Males were more roost site faithful than expected under random settlement whether they held a territory or not (Wilcoxon test comparing mean expected-observed inter-roost distances to zero: territorial: $Z=4.12$, $N=141$, $P<0.0001$; nonterritorial: $Z=3.12$, $N=141$, $P=0.002$). Thus, territoriality affected roost site fidelity on an absolute distance basis but not relative to day range.

Relative positions of territories, hunting areas and roosts

Territorial male rubyspots did not roost at locations that reduced the daily commuting distance between territories and hunting areas, relative to the alternative of roosting on the territory. For the morning roost-to-territory commute, the mean \pm SE distance from roost to hunting area (RH) was 10.6 ± 0.8 m, versus 4.9 ± 0.7 m from hunting area to territory (HT). Thus, the mean morning commuting distance was 15.5 ± 1.1 m, versus

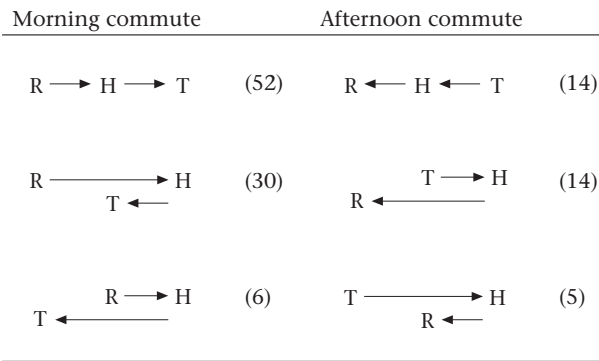


Figure 2. Relative positions of hunting (H), roost (R) and territory (T) sites for males observed either on the morning commute to the territory or the afternoon commute to the roost. Samples sizes in parentheses. Note that the examples illustrated just indicate the relative placement of sites; the 'mirror' image of each (e.g. T–H–R for the morning commute) was also included in the analysis. Expected values were based on each type of site having an equal chance of being between the other two. Morning commute: $\chi^2_2=36.09$, $P<0.0001$; afternoon commute: $\chi^2_2=4.91$, $P=0.10$.

9.8 ± 1.4 m for a round-trip between territory and hunting area (Wilcoxon matched-pairs signed-ranks test of RH+HT versus 2 HT: $Z=6.92$, $N=116$, $P<0.0001$). For the afternoon territory-to-roost commute, the mean distance from territory to hunting area was 12.0 ± 3.3 m, versus 12.4 ± 3.0 m from hunting area to roost. Therefore, the mean afternoon commuting distance was 24.4 ± 5.3 m, versus 24.8 ± 6.0 m for a round-trip between territory and hunting area (Wilcoxon signed-ranks test of RH+HT versus 2 HT: $Z=0.44$, $N=34$, $P=0.66$). Overall, in neither morning nor evening did the roost sites chosen by territorial males significantly reduce their daily commute between hunting areas and territories.

To understand the relative spatial positions of territories, roosts and hunting areas, we tallied the number of males for which the territory, roost, or hunting area was usually central to (located somewhere between) the other two sites. For the morning commute, either the hunting area or the territory most frequently had the central location; rarely was the roost central to the other two sites (Fig. 2). Combined with relative distances presented in the previous paragraph, this result indicates that, in the morning, males generally flew towards the territory from the roost, sometimes passing the territory, before hunting relatively close to the territory. For the afternoon commute, again hunting areas and territories were most likely to be central, but this pattern was not statistically significant (Fig. 2). These results indicate that males did not consistently fly towards the roost, and rarely flew past the roost, to hunt in the afternoon.

Roost site shifts following territory acquisition

Males sometimes acquired a new territory distant (>30 m) from their former day range and roosting sites. Frequently these males returned to their former roosting site on one or more nights before starting to roost near the new territory. These anecdotal observations suggested that roost locations are learned, and that finding new

roosts takes time. To study this phenomenon quantitatively, we examined all cases in which we knew the location of a male's roost for at least 2 days before he acquired a territory and for at least 3 days afterwards, if he continued holding the territory ($N=86$ males). We calculated the distance between the roost site the male entered at the end of each day and the centre of his new territory. We refer to the day of territory acquisition as day 0, the day before territory acquisition as day -1 , the day after territory acquisition as day 1, and so on. A graphical summary of the results is shown in Fig. 3.

Territory gains were not preceded by roost site shifts in the direction of the new territory; males roosted no closer to their new territories on day -1 than on day -2 (Fig. 3a; paired t test: $t_{85}=-0.44$, $P=0.65$). Instead, territory gains were followed by roost site shifts in the direction of the new territory. The number of males roosting more than 20 m from the new territory decreased sharply between day -1 and day 2 (Fig. 3d), and the reduction in territory-to-roost distance over this period was highly significant (Fig. 3b; $t_{85}=4.44$, $P<0.0001$). There was no further reduction in the distance between territories and roost sites from day 2 to day 3 (Fig. 3c; $t_{85}=0.40$, $P=0.69$), although several males continued to roost 30 m or more from their new territory (Fig. 3c).

Experiments

Experiment 1: conspecific attraction

The near absence of recruitment to control sites (Table 1) precluded meaningful statistical comparison of the different control treatments. To test for attraction of rubyspots to the rubyspot models, we pooled the control treatments. Rubyspots settled at one of 33 control sites versus 11 of 33 rubyspot model sites (Table 1; Fisher's exact test: $P=0.003$), demonstrating attraction to the rubyspot models. The median number of animals found at the recruiting rubyspot model sites was 1 (range 1–3); nine of the 15 recruits were male. If only four-model groups are considered, rubyspot models still attracted recruits more frequently than controls (seven of 26 rubyspot model sites versus one of 26 control sites; Fisher's exact test: $P=0.05$).

We examined group size effects by comparing recruitment to rubyspot model groups of size eight to those of size four. All eight-model groups were paired with a vacant control site, so we first compared recruitment to eight-model groups and four-model groups that were also paired with vacant controls. In this comparison, rubyspots settled more frequently by the larger model groups (four of eight eight-model groups recruited versus zero of eight four-model groups; Fisher's exact test: $P=0.02$). In comparison to all four-model groups, however, eight-model groups were not significantly more attractive (Table 1; Fisher's exact test: $P=0.2$).

Experiment 2: development and maintenance of roost sites

Only three of 30 model sites and one of 30 control sites attracted recruits after 1 day, a nonsignificant difference

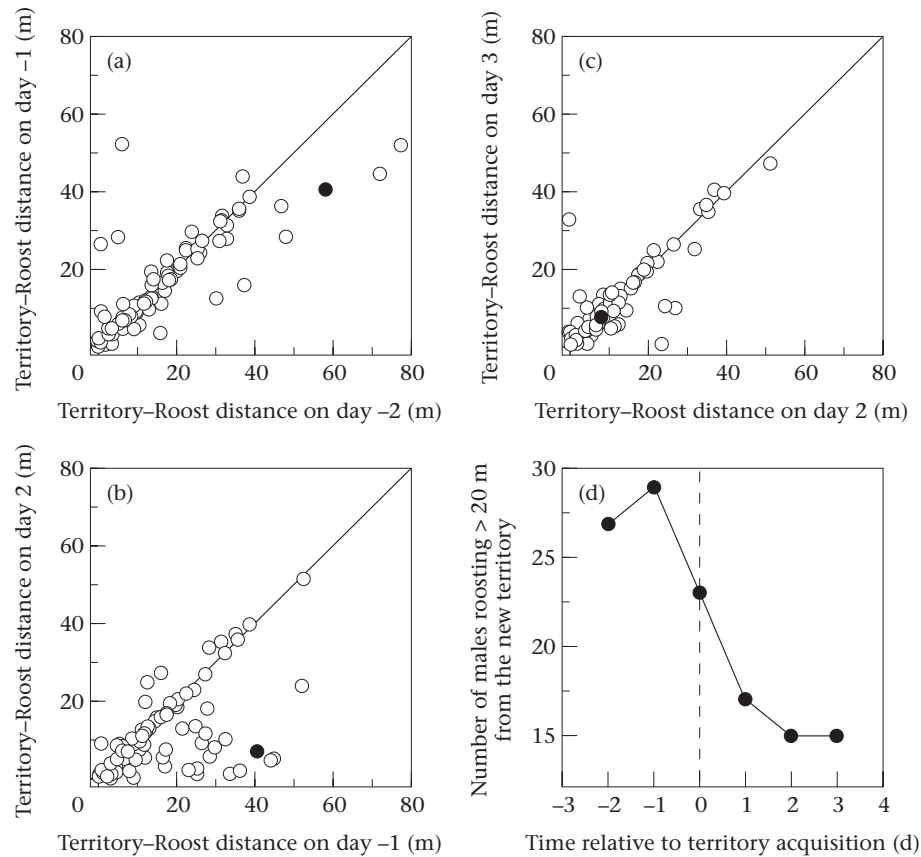


Figure 3. (a–c) Roost site shifts in relation to territory acquisition ($N=86$ males). Day -1 is one day before territory acquisition, day 1 is one day after territory acquisition, and so on. Points below the diagonal $Y=X$ lines indicate that territory-to-roost distances decreased over the corresponding time interval. The filled symbols (a–c) provide an example of an individual that roosted closer to his new territory after territory acquisition than before. Distance between roost site and new territory (a) 1 day before (day -1) versus 2 days before (day -2) territory acquisition, (b) 2 days after (day 2) versus 1 day before (day -1) territory acquisition, (c) 3 days after (day 3) versus 2 days after (day 2) territory acquisition. (d) Number of males roosting more than 20 m from the new territory versus time relative to territory acquisition. See text for interpretation and statistics.

Table 1. Results of conspecific attraction experiment 1

Type of models placed at site	Number of models*	Number (%) of sites with recruits	Total number of sites
Rubyspot	4	7 (26.9)	26
Rubyspot	8	4 (50.0)	8
Vacant control	4	0 (0.0)	9
Vacant control	8	0 (0.0)	8
Clear control	4	0 (0.0)	8
Blue control	4	1 (11.0)	9

See text for statistics and definition of model types.

*For vacant control sites, this refers to the nearest rubyspot model group.

(Fisher's exact test: $P=0.6$). After 1 week, however, 13 of 30 model sites attracted recruits, versus four of 30 of the paired controls (Fisher's exact test: $P=0.01$). Thus, rubyspots were attracted to their model mimics, as in experiment 1, and this effect may have increased over time. After the models were moved on day 7, sham-manipulated sites showed no significant change in

recruitment (Table 2). Control sites that became model sites showed a borderline significant increase in recruitment, with six more sites attracting rubyspots once they contained models (Table 2). Model sites that became control sites showed a significant decrease in recruitment (Table 2), suggesting that these sites were less attractive without the models, but recruitment at these sites remained relatively high. Of the eight model sites with recruits on day 7, four sites (50%) attracted recruits on day 8 when the models were absent, compared with zero of two (0%) control sites that remained controls, and four of five (80%) model sites that retained their models (these sample sizes are too small for statistical comparisons). Thus, although the models continued to be an attractive stimulus for roosting after 8 consecutive days of presentation, the seeded sites frequently continued to be occupied even after the models were removed.

DISCUSSION

Rubyspot damselflies of both sexes usually roosted close to their previous night's roost, but only males were more roost site faithful than expected by chance (under the

Table 2. Effect on recruitment of moving the rubyspot models 1 week after they were originally placed

Treatment (day 7, day 8)	Number of sites recruiting (day 7, day 8)	Mean change in number of individuals	Wilcoxon T (N)	P
Control, control	2, 1	-0.067±0.12	2 (3)	*
Control, model	2, 8	0.87±0.47	7 (9)	0.06
Model, model	5, 8	-0.133±0.70	17 (9)	0.29
Model, control	8, 5	-0.533±0.24	2.5 (7)	0.03

N=15 sites of each type; sample sizes for the Wilcoxon test equals number of sites with a change in the number of recruits.

*Sample sizes were too small to test for statistical significance.

conservative assumption that only roosts within an individual's observed day range were available for that individual to settle). Roost site fidelity increased when males held mating territories, but not after differences in day range between territorial and nonterritorial periods were taken into account. Hence, the apparent greater site fidelity of males than of females cannot be attributed to male territoriality, but it could be an artefact of the relatively short day ranges of females. Most individuals were roost site faithful most of the time, yet roost site shifts of several metres were common (Fig. 1). When males acquired a new territory, they began roosting closer to the territory after a brief delay (Fig. 3). Roosts were not located at sites that reduced the daily commuting distance between hunting areas and territories, however; males generally hunted closer to their territories than to their roosts. Rubyspots were weakly attracted to roost near models of male rubyspots but were not attracted to roost near control models with clear wings (Table 1). Sites seeded with rubyspot models often continued to be used even after the models were removed (Table 2). Below we discuss these results in relation to three themes: (1) costs and benefits of roost site fidelity, (2) factors influencing roost site choice, and (3) mechanisms underlying the formation and maintenance of roost aggregations.

Roost Site Fidelity

Studies of other species have also revealed fidelity to particular roosting sites (Rau & Rau 1916; Wynne-Edwards 1962; Waller & Gilbert 1982; Eiserer 1984; Mallet 1986; Miller 1989) and use of multiple sites (e.g. Jones 1930; Heisterberg et al. 1984; Giroux 1991; Lewis 1995; Marzluff et al. 1996). Individuals may benefit from site fidelity if past experience at a location is correlated with future events (Switzer 1993). Rubyspots returning to a familiar site may be aware of potential hazards (e.g. spider webs) and other environmental factors (e.g. position relative to the sun in the morning; Neubauer & Rehfeldt 1995; Switzer & Grether 2000), and in any case would not have to spend time looking for a suitable roosting site. Less time searching for roosting sites translates into more time for other activities, such as hunting, and reduces the risks involved with assessing sites. Roost locations may also represent the least costly sites in terms of travel distance to

foraging sites and other daytime locations (Caccamise & Morrison 1986; but see below).

Individual rubyspots usually used more than one roosting site over the course of their adult lifetimes (Fig. 1). Switching sites is predicted whenever the long-term benefits of switching exceeds the cost of moving (Switzer 1993; Lewis 1995). For example, pallid bats may switch roosting sites to control ectoparasite loads (Lewis 1996). Nocturnal disturbances, such as excessive wind or predation of roostmates, might also be expected to tip the cost-benefit ratio. In addition, animals may switch roosting sites when they happen to encounter new ones (Heisterberg et al. 1984; Giroux 1991), as would be expected if the costs of switching are negligible.

Our results suggest that territoriality is closely related to roost site fidelity. When males acquired a mating territory distant from their previous roosting site, they usually switched to a roosting site nearer the territory (Fig. 3). Such shifts may serve to reduce travelling costs (e.g. energy, time, predation risk). From an optimality perspective, examination of Fig. 3c suggests that the benefits of changing sites outweighed the costs at commuting distances of 10–15 m. Interestingly, however, some individuals continued to commute 30–40 m for several days after acquiring a new territory. The gradual nature of roost site switches (Fig. 3d) suggests that locating suitable roosting sites takes time or that preferences for previously used sites constrain some males from switching immediately.

Roost Site Choice

In the early literature on avian roosting aggregations, roosts were assumed to be the bases of foraging activity for individual birds. Subsequent studies on marked birds revealed that, in some species, individuals often switched roosts and were more faithful to their diurnal activity centres (DACs) than to their roosts (Caccamise & Morrison 1986). This seemed to contradict the notion that communal roosts could function as centres for sharing of foraging information (but see Marzluff et al. 1996; Marzluff & Heinrich, in press). To explain why communal roosts form in such species, Caccamise & Morrison (1986) proposed that communal roosts are located near rich supplemental feeding areas (SFAs) that are visited before and after the birds spend the day in

their respective DACs. These sites are used for a short time during seasons when individuals benefit from the relatively high energy gains at SFAs. So long as the distance between the communal roost and SFA is shorter than the distance from SFA to DAC, an individual bird could reduce its daily commuting costs by roosting at the communal site, as opposed to roosting near the DAC. Caccamise & Morrison (1986) invoked an antipredation benefit to explain why birds aggregate at small, local roosts but argued that very large, distant roosts were used mainly to lessen the cost of commuting to SFAs. Large roosting aggregations are not a necessary consequence of roosting near SFAs, unless suitable roost sites are limited; however, the spatial and seasonal aspects of Caccamise & Morrison's (1986) hypothesis have been supported for some species (e.g. Caccamise & Morrison 1988; Stouffer & Caccamise 1991; but see King et al. 1995).

Communally roosting territorial male rubyspots behave similarly to DAC-based birds; they hunt away from their territories after leaving the roost in the morning and again before roosting in the evening, and are more site faithful to territories than to roosting sites. We found, however, that males did not roost at locations that reduced the daily distance travelled between roosts, hunting areas and territories, relative to the alternative of roosting on the territory, contradicting a crucial prediction of the patch-sitting hypothesis (Caccamise & Morrison 1986, 1988). Based on the relative spatial positions of territories, roosts and hunting areas (Fig. 2), it appears that males chose a roost near their territory and hunted between these two sites, as opposed to roosting near a hunting area. Thus, rubyspots may violate an (implicit) assumption of the patch-sitting hypothesis: that suitable roosting sites are more available than suitable foraging areas.

During the morning territory-to-roost commute, males actually hunted closer to their territories than to their roosts. This may allow males to keep track of local environmental (temperature, sunlight, etc.) and social (arrival of females and other males) conditions and better time their territorial activity. Because males rarely hunt while defending a territory (G. F. Grether, unpublished data), getting the most out of the limited morning and evening hunting periods may be critical for maintaining energy reserves required for territorial fights (Marden & Rollins 1994) and mating.

As we discuss in more detail elsewhere (Switzer & Grether 2000), roost site preferences in this species may be shaped by a number of selective factors, including the benefits of roosting with conspecifics (e.g. predator dilution), risks associated with roosting at untested sites (e.g. wind, predators), benefits of being warmed by the sun earlier in the morning (e.g. reduced period of vulnerability to predators, lengthened active period), and seasonal changes in vulnerability to floods.

Mechanisms of Roost Site Formation and Maintenance

At a proximate level, the spatial and temporal dynamics of rubyspot roosting behaviour can be explained by four

mechanisms: habitat selection, conspecific attraction, spatial memory and roost site preferences. Together these mechanisms may result in a rudimentary form of cultural transmission.

The consistency with which roosts were found on the west bank of the stream (Switzer & Grether 2000) implies active selection of the west bank. Just prior to roosting, rubyspots hunt from the east bank (perhaps because back-lit prey are more conspicuous) and therefore must cross the stream to roost. The tendency for roosts to be located along pools instead of riffles (Switzer & Grether 2000) might be a passive consequence of the preference for hunting over pools (Grether & Grey 1996), but this still requires habitat selection. Habitat selection cannot explain the tendency of rubyspots to aggregate within the preferred habitat, however. Conspecific attraction, through visual or chemical cues, has been implicated as a mechanism for aggregating at roosts in other species (e.g. Reynierse et al. 1969; Copp 1983; Mallet 1986). Our model experiments provide direct evidence for visual conspecific attraction in rubyspots. Recruitment to the rubyspot models was weak (on average, only one recruit per model group), but given that rubyspots tend to be roost site faithful and that the models were in competition with real animals, strong recruitment to the models was not expected. Together habitat selection and conspecific attraction may explain why aggregations tend to form repeatedly in the same general areas, but additional factors are required to explain the roost site fidelity of individuals and the tendency for large aggregations to form repeatedly at specific sites. Damselflies do not mark the habitat physically or deposit chemical cues (Corbet 1962), so some form of spatial memory (e.g. visual landmarks) may be required to explain how individuals relocate preferred sites. In other contexts, spatial memory appears to be well developed in this species (e.g. males seem to remember the exact locations of their territories; Grether 1996b). A less plausible alternative is that individuals repeatedly select the same sites because of precise microhabitat preferences that vary from animal to animal (i.e. without spatial memory).

Traditional roosting aggregations may be an emergent outcome of the processes described above. When an individual learns the location of a roost site by joining conspecifics, the tradition of roosting at the site is passed along. Drift over time in which sites are most popular for roosting may be attributed to chance alone (i.e. cultural drift: Switzer & Grether 2000). Individuals with strong preferences for particular roosting sites may serve as nuclei around which aggregations form. When such individuals die, the aggregations they seeded may begin to drift or decay. Some evidence for this was provided by our second model experiment. Only half of the rubyspot model sites that attracted recruits were still used after the models were removed (Table 2). Traditional use of particular sites has been documented in other animals. For example, blue headed wrasses, *Thalassoma bifasciatum*, spawn at only a small fraction of the sites (coral heads) that appear suitable, and may even show preferences for degraded coral heads that are suboptimal with respect to spawning success (Warner 1988, 1990). Reef population

translocation experiments have confirmed that these mating site preferences are traditional and not based on habitat cues undetected by the researchers (Warner 1988, 1990). Similar experiments on rubypots could sharpen the distinction between roost traditionality and micro-habitat selection.

Acknowledgments

We thank J. H. Grether for field assistance and A. Smernes, Jr for permission to use the land. I. and J. Switzer provided assistance throughout the study and E. K. Hayashi helped make the damselfly models. P. G. Parker, J. M. Marzluff and an anonymous referee provided helpful comments on the manuscript.

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