Alternative models of conspecific attraction in flies and crabs

Judy Stamps,[a] Richard McElreath,[b] and Perri Eason[c]
[a]Section of Evolution and Ecology, University of California at Davis, 1 Shields Avenue, Davis, CA 95616, USA, [b]Department of Anthropology, University of California at Davis, 1 Shields Avenue, Davis, CA 95616, USA, and [c]Biology, University of Louisville, Louisville, KY 40292, USA

Animals are often attracted to one another when selecting habitats, but little is known about the rules governing conspecific attraction. We use Akaike Information Criterion to evaluate alternative models of the effects of conspecifics on individual choice in the context of habitat selection. One set of models was tested using data collected on virgin female flies, *Drosophila melanogaster*, selecting habitats in the laboratory; a second set of models was tested using data collected on crabs, *Ocypode rotundata*, selecting foraging patches in the field. Patterns of space use in the flies were most consistent with models indicating that individuals were attracted to other females that selected traps during the same hour, as well as to cues left by females that had entered traps during the previous hour. Results for the crabs were most consistent with a model which assumes that individuals preferred to join the patch with the most crabs but that their ability to assess the number of crabs in alternative patches was constrained by basic psychophysical principles (Weber's law). These results provide support for hypotheses about the functional significance of conspecific attraction in the flies and the crabs and illustrate the richness of information about conspecific attraction that can be obtained when the same data set is confronted with alternative models of the ways that animals respond to one another when selecting habitats. *Key words:* AIC, alternative models, conspecific attraction, Weber's law. *[Behav Ecol]*

Functional explanations for conspecific attraction fall into two general categories: individuals benefit from the presence of conspecifics after arriving at a location (i.e., Allee effects; Stamps, 2001; Stephens and Sutherland, 1999) or individuals use the presence of conspecifics as a source of information about the quality of habitats, food, or other salient items in a given area (Danchin et al., 2004; Stamps,1988; Stamps and Krishnan, in press). Thus far, however, most studies of conspecific attraction focus on whether or not it occurs, rather than exploring hypotheses about the adaptive significance of this behavior (e.g., see Muller et al., 1997; Schuck-Paim and Alonso, 2001; Ward and Schlossberg, 2004).

One reason is that empirical studies of conspecific attraction traditionally rely on standard statistical approaches, in which an alternative hypothesis (namely, that animals are attracted to conspecifics in a given situation) is tested against a null hypothesis (that individuals are not attracted to conspecifics in that situation). Alternative statistical techniques allow more sophisticated analyses of this phenomenon. These approaches involve identifying several different models of biologically reasonable hypotheses, testing these models using the same data set, and then selecting the model which best fits the data (Anderson et al., 2000; Burnham and Anderson, 2002; Hilborn and Mangel, 1997).

The advantages and disadvantages of null hypothesis statistical approaches versus multimodel approaches have been the subject of lively discussion and debate for a number of years (review in Gigerenzer et al., 2004). Some authors, including Anderson et al. (2000), Burnham and Anderson (2002), and Hilborn and Mangel (1997), strongly encourage multimodel approaches, while others suggest that these new approaches complement, but do not replace, null hypothesis testing (e.g.,

see Chow, 1998; Mogie, 2004). One indication that biologists have found multimodel approaches useful is the recent upsurge in these statistical techniques in ecology, psychology, and other fields related to animal behavior. However, with a few notable exceptions (e.g., Luttbeg and Langen, 2004; Skalski and Gilliam, 2002), behavioral ecologists have not taken advantage of these techniques. The current study demonstrates how confronting the same data with alternative models can be used to study conspecific attraction in two contexts: habitat selection by flies (*Drosophila melanogaster*) and foraging patch selection by ghost crabs (*Ocypode rotundata*).

Conspecific attraction in adult *D. melanogaster* is usually assumed to function in the location of mates or oviposition sites (e.g., Amrein, 2004; Lefranc et al., 2001). This assumption is based on observations suggesting that mature adult males and mated females are attracted to one another (Lefranc et al., 2001; Osses, 1998) and evidence that mature males produce an aggregation pheromone, *cis*-vaccenyl acetate (cVA), which is passed to females during mating and released with the eggs (Bartelt et al., 1985).

Recently, however, Wertheim et al. (2002) demonstrated that the growth and survivorship of larvae in a freshly cut fruit is enhanced if multiple virgin females have previously been allowed access to that fruit. He suggested that groups of female *Drosophila* might inoculate fresh fruits with beneficial yeasts and other microbes, thereby encouraging the development of microbial communities which will eventually provide high-quality food for their offspring. In turn, if multiple females improve habitat quality for their offspring, one would predict that virgin females would be attracted to other virgin females at a fresh food substrate and that virgin females would be sensitive to a range of cues (visual, olfactory, etc.) indicating the presence of other virgin females at a fresh food source. Because females associated with a particular fruit spend a large proportion of their time perched at locations away from that fruit (Stamps et al., in press), we were particularly interested in the possibility that virgin females might be able to detect

Table 1

Protocols for experiments of conspecific attraction using virgin female *Drosophila melanogaster*

| Experiment | Natal habitat | Postdispersal habitats | | Number of trials |
		Trap 1	Trap 2	
1	Kiwi-Leaf	Kiwi-Leaf	Banana-Wire	17
2	Banana-Wire	Kiwi-Leaf	Banana-Wire	22
3	No food-Shavings	Kiwi-Leaf	Banana-Wire	9
4	Laboratory medium-Shavings	Kiwi-Leaf	Banana-Wire	6
5	Banana-Wire	Aged banana-Wire	Fresh banana-Wire	8

For natal and the postdispersal habitats, we first indicate the food at the site, followed by the type of structural features at that site.

cues left behind by other females that had previously visited a fruit. Hence, the hypothesis that Allee effects occur in *D. melanogaster* yields several predictions about conspecific attraction in virgin females.

Preliminary observations of ghost crabs indicated that newcomers were strongly attracted to other individuals at food items (Eason P, unpublished data), so in this case, we focused on the rules that individuals might use to determine which foraging patch to join. Joining rules for conspecific attraction are important because they determine the functional relationship between the number of animals in a patch and the chances that a new arrival will join that patch. For instance, observations that the tendency of foraging individuals to join a group increases as a function of group size (Krebs, 1974; Murton et al., 1966; Pöysä, 1991; Wood, 1985) are consistent with two hypotheses: new arrivals use the number of conspecifics in a patch to assess patch quality or individuals benefit by foraging in larger groups. Interestingly, however, when groups of very different sizes co-occur within the same study area, the relationship between attractiveness and group size is asymptotic (Krebs, 1974; Murton et al., 1966; Wood, 1985), for reasons that are currently obscure (Pöysä, 1991).

One possible explanation for an asymptotic relationship between attractiveness and group size is that animals prefer to join larger groups but the ability of animals to count conspecifics is constrained by general laws of psychophysics. In particular, linear increments in sensation are proportional to the logarithm of stimulus magnitude, a relationship known as Weber's law, or the Weber-Fechner law. Animal estimates of numerosity conform to this law (Shettleworth, 1998), and recent studies indicate that the nonlinear, compressed "number scale" of animals may be directly related to the nonlinear system by which neurones code numerical values (Dehaene, 2003; Piazza et al., 2004). Hence, we studied several plausible joining rules for crabs, one of which specifies that the attractiveness of a patch increases as a function of the number of individuals in the patch but that the ability of crabs to count conspecifics is constrained by Weber's law.

METHODS

Flies

Experiments

The experimental subjects were five recurrent F1s, each of which was produced by crossing two different female isolines (for details, see Stamps et al., in press). Each F1 is here indicated by X/Y, where X is the maternal isoline and Y the paternal isoline.

In order to determine whether patterns of conspecific attraction for virgin females varied as a function of conditions at their natal site or conditions at postdispersal sites, we con-

ducted five experiments. These experiments varied with respect to the food situation and structural features at the natal and/or the postdispersal sites. The experiments were conducted in an animal room ($2.6 \times 2.6 \times 3.6$ m), under a 11:13 h light:dark cycle (lights on at 0900 h, off at 2000 h), with an average temperature and humidity of 25°C and 68%, respectively.

Female pupae from one of the F1s were collected from vials in which they had been raised in laboratory medium and allowed free access to a "natal habitat" for their first day of adult life, as described in Stamps et al. (in press). In brief, on the evening of Day 0, two vials were either provisioned with 10 ml of "conditioned food" or left empty (no food). Conditioned food consisted of kiwi fruit, banana, or dextrose medium, which had previously been used for foraging, oviposition, and larvae development by flies from a single isoline (#755). Eleven female pupae from one of the five genotypes were lightly painted with liquid from the conditioned food and then placed on netting within each vial. Then, the two vials were placed side by side in structural features located in the animal room. Three types of structural features were used: Leaf, a 1000-ml beaker with green plastic leaves and wooden dowels; Wire, a 1000-ml beaker with brown plastic wire and dowels; or Shavings, pine shavings with short sections of wooden dowels. The food and structural features to which the newly emerged females were exposed during their first day of adult life in each of the five experiments are indicated in Table 1.

At 0830 h on Day 2, any females remaining in the vials or the surrounding structural features were induced to leave by gentle shaking, the vials and structural features were removed from the room, and two new "postdispersal" habitats were placed 3 m apart on a table in the room. Each new habitat included a trap with clear plastic walls and a netted funnel at the top, within which was a single piece of fruit. Three types of fruit were used in the experiments: a freshly cut slice of banana, a freshly cut slice of kiwi, or an "aged" slice of banana (cut 48 h before being placed in the trap). Each trap was surrounded by structural features, either Leaf (green plastic leaves supported on a framework of wooden dowels) or Wire (lengths of brown plastic wire supported by a framework of wooden dowels). The types of food and structural features used for the postdispersal habitats in each experiment are indicated in Table 1.

We counted the number of females entering each of the two traps in each experiment each hour from 0900 to 2000 h on Day 2 and Day 3 and from 0900 to 1700 h on Day 4. After females had been counted, they were released outside of the animal room, and the traps were replaced in their original positions. At the end of each trial, the vials, structural features, and traps were thoroughly washed with water prior to the beginning of the next trial. For Experiments 1–4, the five F1s were tested on a rotating basis, and each of the F1s contributed approximately the same number of trials to the final results. Experiment 5 focused on two F1s: 17/15 and 147/148.

Models

For each of the five experiments, we tested four different models of conspecific attraction. These logit models predict the probability that a fly would φ enter Trap 1, based on other parameters specific to each model.

Model 1: Independent Search (IND). This model assumes that the decisions made by each fly are independent of those made by other flies. For fly i, the probability of entering Trap 1 is given by:

$$\Pr_i(1) = \frac{1}{1 + \exp(p)} = \phi,$$

where p is fit from the data and reflects the relative attractiveness of Trap 1 versus Trap 2 for all the flies in the experiment.

Model 2: Follow First (FF). This model assumes that the flies in each trial were attracted to the first fly that selected a trap in their trial. A new parameter β captures this attraction. Let the probability of fly i entering Trap 1 after the first fly has entered Trap 1 be:

$$\Pr_i(1|1) = \frac{1}{1 + \exp(p + \beta)} = \phi^+. \quad (1)$$

Likewise, the probability that fly i enters Trap 1 after the first fly has entered Trap 2 is:

$$\Pr_i(1|0) = \frac{1}{1 + \exp(p - \beta)} = \phi^-. \quad (2)$$

The unconditional probability of fly i entering Trap 1 is now:

$$\Pr_i(1) = \frac{1}{N}\phi + \frac{N-1}{N}\left(\frac{n_1 - c_i}{N-1}\phi^+ + \frac{n_2 - (1-c_i)}{N-1}\phi^-\right),$$

where n_j is the number of flies that was observed to enter Trap j during the interval under consideration, $N = n_1 + n_2$ is the total number of flies in the interval and c_i is the trap fly i actually chose, $=1$ for Trap 1 and $=0$ for Trap 2.

The first term of this equation captures the movement of the first fly that cannot be influenced by any of the others. The first fly is therefore governed by the independent search model (IND). Because any of the N flies could have been the first (we do not know), there is a chance $1/N$ that fly i was the first. The second term is the remaining $N-1$ flies. For each of these, we first consider what the first fly did. The first fly could have been either in Trap 1 or in Trap 2. We select a fly at random from all the flies collected in the hour, except fly i. Thus, for example, if there were three flies collected, and two entered Trap 1 and one entered Trap 2, then either fly that entered Trap 1 could have followed either a first fly in Trap 1 or Trap 2. Thus, there is a half chance of either. The fly that entered Trap 2, however, must have followed a fly in Trap 1, if she was not the first fly.

When $\beta < 0$, flies are attracted to the first fly. When $\beta > 0$, flies avoid the first fly.

Model 3: Hour-lag Attraction (HL). This model assumes that the decisions of flies in a given hour are affected by cues left behind by flies that visited traps the previous hour. In particular, we assumed that the ratio of flies in Trap 1:Trap 2 the previous hour affected the choices of flies during the current hour. We model the influence of the ratio as:

$$h = 2\delta(T^- - 0.5),$$

where $T^- = n_1^-/N^-$ is the proportion of flies from the previous hour that entered Trap 1 (the hour-lagged proportion of flies in Trap 1). The parameter δ measures the strength of the influence of T^-, which is assumed to depend on the ratio, not the absolute difference in numbers (see discussion on Weber's law, Introduction). If the proportion from the previous hour

was 0.5, then there is no net influence of behavior from the previous hour. Similarly, when $\delta = 0$, flies ignore cues from the previous hour.

The probability of a fly i entering Trap 1 is then:

$$\Pr_i(1) = \frac{1}{1 + \exp(p - h)}.$$

Thus, when $h > 0$, more flies in Trap 1 from the previous hour attract flies to Trap 1. When $h < 0$, flies in Trap 1 from previous hour repel flies from Trap 1.

Model 4: Follow First + Hour-lag (FF-HL). This model combines Models 2 and 3. h is computed as in Model 3, and p in Model 2 becomes $p' = p - h$. Thus, just substitute for φ in Model 2:

$$\phi' = \frac{1}{1 + \exp(p - h)}.$$

Model fitting

In preliminary analyses, we fitted models by experiment and genotype (F1). These analyses confirmed earlier suspicions that each experiment type needed to be fit separately because the parameter p varied across the experiments (see Table 2). In other words, the attractiveness of Trap 1 relative to Trap 2 varied as a function of conditions in the natal habitat and conditions at the new postdispersal habitats. However, we were unable to detect any sizeable or consistent effect of genotype on any of the results. Accordingly, in this study, we combined data from the different F1s and then determined model fits separately for each of the five experiments.

For each experiment and model, we computed the log likelihood that each of the four models correctly described the choices made by the individuals in that experiment. These log-likelihood values were then used to compute the value of Akaike's information criterion (AIC) for each experiment and model (see Burnham and Anderson, 2002). An AIC value (defined as twice the negative log likelihood plus twice the number of parameters in the model) provides an estimate of the relative distance between a fitted model and the unknown true mechanisms that generated the observed data. For any given data set, models with smaller AIC values are more likely to reflect the true underlying mechanisms than models with larger AIC values.

Note that in addition to varying as a function of log-likelihood values, AIC values also depend on the number of parameters in a model. This is because adding extra parameters to a model virtually always improves the fit of a model to the data. Hence, the issue is whether adding a parameter to a model increases its fit to the data, over and above the extent of improvement expected even if that parameter captured no actual structure in the data. Looking at it another way, differences in AIC values reflect differences in the ability of the models to predict the results in the data set, after adjusting for the degree of fit expected on the basis of the complexity of each model.

As with many statistics, the absolute magnitude of AIC is less informative than the relative values across different candidate explanatory models. Thus, statisticians compare the relative magnitudes of AIC. This is most easily done with "Akaike weights." The Akaike weight w_x for a model x in a set of n models given by:

$$w_x = \frac{\exp[-0.5(\text{AIC}_x - \text{AIC}_{\min})]}{\sum_{i=1}^{n}\exp[-0.5(\text{AIC}_i - \text{AIC}_{\min})]}.$$

This quantity ranges from zero to one, higher values indicating better comparative fit to data. Akaike weights quantify relative support of each model (Burnham and Anderson, 2002).

Table 2
Models fitted to fly experiments[a]

Experiment	N	Model	Measures of fit			Parameter estimates		
			AIC	w	D	p	β	δ
1	345	IND	294.535	0.018	0.39	-1.7289		
		FF	287.706	0.541	0.41	-1.4174	-1.2078	
		HL	293.195	0.035	0.40	-1.5235		0.4301
		FF-HL	288.280	0.406	0.41	-1.2919	-1.0793	0.3047
2	455	IND	632.498	4.52×10^{-28}	0.00	.0484		
		FF	514.305	0.021	0.19	$-.0177$	-3.2603	
		HL	570.574	1.26×10^{-14}	0.10	$-.0052$		1.0327
		FF-HL	506.612	0.979	0.21	$-.0046$	-2.2605	0.6179
3	129	IND	175.956	0.006	0.03	$-.3926$		
		FF	167.546	0.419	0.09	$-.4156$	-1.7481	
		HL	174.113	0.016	0.05	$-.3178$		0.5813
		FF-HL	166.968	0.559	0.10	$-.3149$	-1.6789	0.5985
4	104	IND	53.297	0.032	0.64	-2.6288		
		FF	50.892	0.108	0.67	-1.9505	-2.3089	
		HL	49.047	0.271	0.69	-2.1283		1.5150
		FF-HL	47.496	0.589	0.71	-1.4783	-2.2949	1.4278
5	139	IND	194.688	1.37×10^{-10}	0.00	.0144		
		FF	153.072	0.149	0.23	$-.1285$	-4.2808	
		HL	167.932	8.86×10^{-05}	0.15	.1712		1.3468
		FF-HL	149.595	0.850	0.25	.0124	-2.4791	0.9142

[a] The table presents the model fitting results from each of the five experiments, with sample sizes (N). For each model, we show three measures of fit: AIC, Akaike weight (w), and D (fit relative to random model). Maximum likelihood parameter estimates follow for each model. See text.

After AIC values have been computed for all the models which are fit to a given data set, Akaike weights associated with each model are used to evaluate which of these models best represents the underlying processes. Some statisticians interpret Akaike weights in a probabilistic fashion: the number indicates the approximate number of times the model would have the lowest AIC in a large number of repeat trials (experiments) on the same population. Bootstrap analysis supports this interpretation (Burnham and Anderson, 2002).

In addition to using AIC to compare models of the effects of conspecifics on choice, we also compute a measure, D, which reflects the overall predictive value of each model. D is analogous to the measure R^2 provided by linear regression. In the current study, D reflects the predictive power of each model, relative to a model in which individuals were assumed to select traps entirely at random. Given the design of the current study, the probability that a fly would randomly select Trap 1 rather than Trap 2 was 0.5, so that the fit of a random model is given by $LL_{random} = N \log(0.5)$, where $N =$ the total number of observations. Hence, the value of D for model x is

$$D_x = 1 - \frac{LL_x}{LL_{random}}.$$

D is a useful accessory to AIC because a model may be the best in a given set but still explain only a small fraction of variance in behavior. D ranges from zero, when model x has the same fit as the random model (the worst any model can do), to one, when model x perfectly predicts all the variance in the data. Thus, in the current study, D provides an indication of how well each model predicted the choices made by all the individuals in the experiment. Like R^2, D should not be used to rank or select models because it almost always increases as one adds additional parameters to a model.

Crabs

Ghost crabs *O. rotundata* were studied at a beach near Ras as Sawadi, Sultanate of Oman (23° 45′ N, 57° 48′ E). This beach supports a high density of crabs (more than 550 individuals per 100 m of shoreline [Eason P, unpublished data]). The crabs emerge from their burrows when large areas of wet sand are available (Vannini, 1976) and primarily forage by deposit feeding and scavenging on larger resources that wash up on to the beaches (e.g., dead fish or turtles) (Eason P, unpublished data).

We ran trials between 1500 and 1830 h on 7 days between 31 May 2003 and 29 June 2003. As a food source, we used pieces of dry cat food moistened with chicken broth. For each experiment, we set out two 1×1–m patches located 6 m apart from one another from center to center. The two patches were oriented parallel to the shoreline and approximately 15 m from the water; the Right patch was to the right for a human observer facing the water and the Left patch to the left. Within each patch, we placed two pieces of cat food every 10 cm, so that there were 11 rows and 11 columns of cat food in each patch. New arrivals were considered to have chosen one of the two patches when they moved inside of a circle located 1 m from the center of the food patch.

In order to avoid sampling the same individuals, after we finished one trial, we moved approximately 50 m along the beach before setting up the next trial. This practice, combined with the large numbers of crabs present in the study area (see above), made it unlikely that any individuals were sampled in more than one trial.

In each of 13 trials, the food patch visited by the first crab was videotaped, while an observer sitting approximately 15 m away from the food patches recorded data for the crabs that arrived at the other patch. Preliminary observations indicated that crabs ignored a still human; indeed, crabs frequently walked right next to the observer. For each crab, we recorded which patch it chose (Left or Right), the time at which it reached that patch, and the number of crabs in each of the two patches when the crab arrived at the patch it selected. All crabs within 1 m of the center of the patch were considered to be in the patch.

Models
The basic model assumes that the chance that a crab will select a patch is independent of the decisions made by other

crabs but is simply affected by the change in odds, α, that a crab will select the Left rather than the Right food patch. To control for potential variation in the attractiveness of Left and Right patches, we allowed α to vary as a free parameter and included an estimate of α in each model.

Model 1: Independent Choice (IND). This model assumes that crabs select patches independently of one another. The probability that crab i chooses the Left (L) patch is given by:

$$\Pr_i(L) = \frac{1}{1 + \exp(\alpha)}.$$

This is a simple logit, as was used for the fly data. The four other models assume that the chances that a crab will select the Left patch depend not only on α but also on cues derived from other crabs. In these cases, the equation becomes:

$$\Pr_i(L) = \frac{1}{1 + \exp(\alpha + \beta V)},$$

where different rules yield different values of V. Details of the four models of conspecific attraction are provided below.

Model 2: Lag1. This model assumes that individuals which selected a patch at time step t observed other crabs and followed the crab that selected a patch during the previous time step $(t-1)$. For this model, for each crab that selected a patch at time t, $V = 1$ if the crab that selected a patch at $(t-1)$ went Left, $V = -1$ if the previous crab went Right, and $V = 0$ if no crab selected a patch during the time interval $t-1$.

Model 3: MajorityLR. This model assumes that when selecting a patch, crabs estimate which of the two patches currently contains the most crabs and then use this estimate when deciding which patch to join. For this model, $V = 1$ if there were more crabs on the Left, $V = -1$ if there were more crabs on the Right, and $V = 0$ if the number of crabs on the Left and Right was the same or if the crab was the first arrival at either patch.

Model 4: DiffLR. This model assumes that when individuals select a patch, they estimate the number of crabs in the Left and Right patches and use the difference between these numbers when selecting one of the two patches. In this case, $V =$ the difference in the number of crabs at the Left and the Right patch when each individual selected a patch.

Model 5: RatioLR. This model assumes that crabs follow the Weber's law when estimating the number of crabs in the Left and Right patches. The ratio of the number of crabs on the Left and the Right (L/R) = (logL − logR). Hence, L/R reflects the difference in the number of individuals that crabs would perceive in the Left and Right patches if their estimates of numerosity followed Weber's law. For the current analysis, we took the natural logarithm of (L/R), to balance the span of data on the left and right sides of zero.

Model fitting
Preliminary analyses indicated no variation in results as a function of trial number, so data from all the trials were combined in the analyses. Initial analysis indicated that the behavior of the crabs changed when 31 crabs had selected the food patches, so we focused on individuals that selected a patch before the 31st crab arrived at either of the two patches. The 13 trials yielded a total of 358 data points, which were fitted to each of the five models indicated above.

For each of the five models, we computed the log likelihood that the model correctly described the choices made by the crabs and then computed the AIC values and Akaike weights for each model. D values were computed based on the assumption that crabs selecting patches entirely at random would be equally likely to select the Left and Right patches.

RESULTS

Flies

Across the five experiments, there was support for two models of conspecific attraction (FF and FF-lag) for virgin female *D. melanogaster* (Table 2). In every experiment except Experiment 1, FF-lag had the best-adjusted fit, as indicated by the fact that the FF-lag model had the lowest AIC values and the highest Akaike weights. However, in two experiments (Experiment 1 and Experiment 3), the Akaike weights were comparable for the FF-lag and the FF model. This suggests that the explanatory power of the hour lag effect is small relative to the explanatory power of within-hour conspecific attraction. This can be seen by noticing that the Akaike weights for within-hour attraction alone (FF) are greater than those of hour-lag attraction alone (HL) in four out of five experiments. Conversely, there was little support for the hypothesis that virgin female *D. melanogaster* selected traps independent of one another. In all five experiments, the AIC values for the IND model were higher, and the Akaike weights lower, than those for the best-fitting conspecific attraction models.

The D values tell a similar story. In every experiment, the highest D values were generated by the FF-lag model, and the lowest D values were generated by the IND model. However, across the experiments, most of the D values were relatively low, indicating considerable unexplained variation in the flies' behavior. This illustrates the important distinction between identifying the best model from a set of models and the ability of that best model to describe all the patterns in a data set.

Crabs

Our results verify that crabs were strongly attracted to conspecifics when selecting foraging locations: all the models of conspecific attraction yielded AIC values much smaller than the AIC value for the IND model (Table 3). Of the four models of alternative rules for conspecific attraction, the best-fitting model, by a very wide margin, was the RatioLR model, which assumes that the attractiveness of a patch to the crabs is positively affected by the ratio of the number of crabs in the Left and the Right patches at the time when the crab selected a patch. The Akaike weights for the other three models are very small, indicating very little relative support. Despite the very high Akaike weight of the RatioLR model, however, its D value of 0.40 indicates that there is still considerable unexplained variance among crabs in patch choice. Hence, as was the case with the flies, the most strongly supported model in a set of models may not necessarily explain most of the variance in that data set.

Table 3
Model fits for crab data[a]

Model	Measures of fit			Parameter estimates	
	AIC	w	D	α	β
IND	468.43	9.37×10^{-37}	0.06	0.6104	
Lag1	337.68	2.31×10^{-8}	0.33	0.3761	−1.4532
MajorityLR	331.78	4.43×10^{-7}	0.34	0.1108	−1.5735
DiffLR	326.09	7.60×10^{-6}	0.35	0.3116	−0.2187
RatioLR	302.52	$1.00 + 00$	0.40	0.4200	−0.4667

[a] $N = 358$ observations. For each model fit the crab behavioral data, we present the same three measures of fit we presented for the fly data. Maximum likelihood parameter estimates follow the measures of fit for each model.

DISCUSSION

By comparing multiple (nonnull) hypotheses, we have tried to understand which of the several plausible processes may account for conspecific attraction in these two systems. Instead of simply asking whether or not virgin female *D. melanogaster* or *O. rotundata* crabs were attracted to one another, the multimodel approach described here allowed us to address more detailed questions about conspecific attraction in both species.

In the flies, our results indicate that virgin females were not only attracted to other virgin females located at fresh food substrates during the same hour but also to cues (probably olfactory) left behind by virgin females that had entered the traps the previous hour. The latter results are interesting because virgin females lack access to the long-distance aggregation pheromone, cVA. However, studies using adult male bioassays show that virgin females produce a volatile pheromone which can be detected by conspecifics (Tompkins et al., 1980; Venard and Jallon, 1980). Attraction of virgin female flies to one another is consistent with the hypothesis that groups of females may be able to enhance habitat quality for their offspring (Wertheim et al., 2002) and imply that the benefits of conspecific attraction in *D. melanogaster* may extend beyond mate attraction and the location of high-quality oviposition sites.

In the crabs, the best model of the rules governing conspecific attraction is one which assumes that the attraction of the crabs to two foraging patches is positively related to the ratio of the number of crabs in those two patches. It is doubtful that crabs benefit by foraging in groups because crabs foraging at rich resource patches are highly aggressive to one another (Burggren and McMahon, 1988; Eason P, unpublished data). A more plausible hypothesis is that crabs use the relative number of conspecifics at a foraging patch to estimate the relative quality of that patch but that their ability to count conspecifics is constrained by Weber's law. Similar asymptotic relationships between foraging group size and the tendency of newcomers to join a group have been reported in other animals (see Introduction). We predict that this same asymptotic relationship will be observed in other situations in which conspecific attraction varies as a function of group size and in which individuals are confronted with a wide range of group sizes (e.g., group sizes that differ by an order of magnitude or more).

Of course, in the current experiment, the tendency of crabs to be attracted to the patch with the most foragers produced suboptimal foraging behavior because most animals competed with conspecifics for access to food in one patch while ignoring an adjacent patch filled with food items. However, under natural conditions, in which ephemeral food items of a wide range of sizes and quality are used by the crabs, individuals might reasonably expect large aggregations of foraging crabs to be indicative of higher food quantity or quality. If the probability of finding another food patch is sufficiently low, foraging with competitors might be the best option.

As is always the case with empirical research, our conclusions are limited by our ability to construct plausible models to explain patterns in the data. Just as there is no guarantee that the alterative hypothesis in null hypothesis testing is the "correct" hypothesis, there is no guarantee that a multimodal approach necessarily includes the model which best reflects the processes responsible for generating the patterns in that data set. For instance, it is possible that we have overlooked a joining rule for the crabs that fits their data better than any of the rules used in the current study.

However, a major advantage of the multimodel approach is the ease with which one can determine whether a new hypothesis fits a data set better than any of the hypotheses previously confronted with that data set (e.g., Luttbeg and Langen,

2004). For instance, if a new hypothesis about conspecific attraction predicts a new joining rule for crabs, it would be a simple matter to compute AIC statistics for a model based on that rule and then compare these to the values obtained in the current study. Thus, the multimodel approach not only encourages researchers to consider a number of different hypotheses when they first analyze their data but also encourages them to remain open to new hypotheses that might provide better explanations for their data in the future.

REFERENCES

Amrein H, 2004. Pheromone perception and behavior in *Drosophila*. Curr Opin Neurobiol 14:435–442.
Anderson DR, Burnham KP, Thompson WL, 2000. Null hypothesis testing: problems, prevalence and an alternative. J Wildl Manage 64:912–923.
Bartelt RJ, Schaner AM, Jackson LL, 1985. Cis-vaccenyl acetate as an aggregation pheromone in *Drosophila melanogaster*. J Chem Ecol 11:1747–1756.
Burggren WW, McMahon BR, 1988. Biology of the land crabs. Cambridge: Cambridge University Press.
Burnham KP, Anderson DR, 2002. Model selection and multimodal inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag.
Chow SL, 1998. Précis of "statistical significance: rationale, validity and utility." Behav Brain Sci 21:169–194.
Danchin E, Giraldeau LA, Valone TJ, Wagner RH, 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487–491.
Dehaene S, 2003. The neural basis of the Weber-Fechner law: a logarithmic mental number line. Trends Cogn Sci 7:145–147.
Gigerenzer G, Krauss S, Vitouch O, 2004. The null ritual: what you always wanted to know about significance testing but were afraid to ask. In: Sage handbook of quantitative methods for the social sciences (Kaplan D, ed). Thousand Oaks, CA: Sage.
Hilborn R, Mangel M, 1997. The ecological detective: confronting models with data. Princeton, New Jersey: Princeton University Press.
Krebs JR, 1974. Colonial nesting and social feeding as strategies of exploiting food resources the great blue heron (*Ardea herodias*). Behaviour 51:99–134.
Lefranc A, Jeune B, Thomas-Orillard M, Danchin E, 2001. Non-independence of individuals in a population of *Drosophila melanogaster*: effects on spatial distribution and dispersal. C R Acad Sci Ser III Sci Vie 324:219–227.
Luttbeg B, Langen TA, 2004. Comparing alternative models to empirical data: cognitive models of Western Scrub Jay foraging behavior. Am Nat 163:263–276.
Mogie M, 2004. In support of null hypothesis significance testing. Proc R Soc Lond B 271:S82–S84.
Muller KL, Stamps JA, Krishnan VV, Willits NH, 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). Am Nat 150:650–661.
Murton RK, Isaacson AJ, Westwood NJ, 1966. The relationships between wood-pigeons and their clover food supply and the mechanisms of population control. J Appl Ecol 3:55–96.
Osses ED, 1998. Aggregation tendency in small groups of *Drosophila melanogaster*. Genet Mol Biol 21:25–30.
Piazza M, Izard V, Pinel P, Bihan DL, Dehaene S, 2004. Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron 44:547–555.
Pöysä H, 1991. Effects of predation risk and patch quality on the formation and attractiveness of foraging groups of teal, *Anas crecca*. Anim Behav 41:285–294.
Schuck-Paim C, Alonso WJ, 2001. Deciding where to settle: conspecific attraction and web site selection in the orb-web spider *Nephilengys cruentata*. Anim Behav 62:1007–1012.
Shettleworth S, 1998. Cognition, evolution and behavior. New York: Oxford University Press.
Skalski GT, Gilliam JF, 2002. Feeding under predation hazard: testing models of adaptive behavior in stream fish. Am Nat 160:158–172.
Stamps JA, 1988. Conspecific attraction and aggregation in a territorial species. Am Nat 131:329–347.

Stamps JA, 2001. Habitat selection by dispersers: proximate and ultimate approaches. In: Dispersal (Clobert J, Danchin E, Dhondt A, Nichols J, eds). New York: Oxford University Press; 243–260.

Stamps JA, Buechner M, Alexander K, Davis J, Zuniga N, in press. Genotypic differences in space use and movement patterns in *Drosophila melanogaster*. Anim Behav.

Stamps JA, Krishnan VV, in press. Non-intuitive cue use in habitat selection. Ecology.

Stephens PA, Sutherland WJ, 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol 14:401–405.

Tompkins L, Hall JC, Hall LM, 1980. Courtship-stimulating volatile compounds from normal and mutant *Drosophila*. J Insect Physiol 26:689–697.

Vannini M, 1976. Researches on the coast of Somalia. The shore and dune of Sar Uanle. 10. Sandy beach decapods (Decapoda Brachyura). Monit Zool Ital 14:57–101.

Venard R, Jallon JM, 1980. Evidence for an aphrodisiac pheromone of female *Drosophila*. Experientia 36:211–212.

Ward MP, Schlossberg S, 2004. Conspecific attraction and the conservation of territorial songbirds. Conserv Biol 18:519–525.

Wertheim B, Marchais J, Vet LEM, 2002. Allee effect in larval resource exploitation in *Drosophila*: an interaction among density of adults, larvae and micro-organisms. Ecol Entomol 27:608–617.

Wood CC, 1985. Aggregative response of common mergansers (*Mergus merganser*): predicting flock size and abundance on Vancouver Island streams. Can J Fish Aquat Sci 42:1259–1271.