

Process-based approach reveals directional effects of environmental factors on movement between habitats

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Summary

1. Understanding the effects of environmental factors on animal distributions is a central issue in ecology. However, movement rules inferred from distribution patterns do not reveal the processes through which animal distribution is realized.
2. We investigated individual movement rules using a process-based approach. In experiments, coastal fish larvae (red drum, *Sciaenops ocellatus*) were matched with an intraspecific competitor of different sizes, and time series of habitat transition of individuals were fitted with a continuous-time Markov chain model to evaluate the effects of the presence of a competitor, behavioural interactions and habitat quality on the likelihoods of habitat transition.
3. The process-based approach revealed that these factors did not simply act as a ‘slope’ between habitats that makes it easier to go in one direction and more difficult to return. Rather, these factors modify the movement rules differently depending on the directions of the movement.
4. Individuals were less likely to enter a better habitat in the presence of a larger conspecific, more likely to shift to a poorer habitat when they received aggressive behaviour and more likely to stay in a better habitat in the presence of food. However, no effect was found on the transition intensity for moving in the opposite direction.
5. The process-based approach to evaluating movement rules of animals allowed us to see the contrasting directional effects of different factors on the underlying movement rules used by animals, as opposed to pattern-based fitting of observed distributions. Consideration of these rules would improve the existing habitat-choice models.

Key-words: aggression, animal distribution, asymmetric competition, habitat selection, interference, light, vigilance

Introduction

Habitat choice has been a major focus for theoretical and empirical ecologists, as it is a key component that connects individual behaviour to community and evolutionary ecology. The classic ideal free distribution (IFD) model (Fretwell & Lucas 1969) predicts that exploitative food competition leads to an asymptotic animal distribution where no individual can increase its energy intake by shifting to another patch. The IFD model has been extended by including important biological factors, such as asymmetric interference competition (Parker & Sutherland 1986; Humphries, Ruxton & Van der Meer 2001), predation risk (Moody, Houston & McNamara 1996) and information on patch quality (Hugie &

Grand 1998; Cressman & Křivan 2006). Numerous studies have tested the assumptions of these models by comparing the predictions with the animal distributions observed in experiments and in nature. However, movement rules in the models are often inferred from the patterns in observed distributions, which do not inform the decision-making processes of animals. An important step forward in developing a full process-based approach (as opposed to pattern-based fitting) is to enhance habitat-choice models through a deeper understanding of the underlying movement rules adopted by animals.

Empirical studies have revealed the influence of various traits and conditions on habitat competition, such as body size (Nakano 1995), aggressiveness (Holbrook & Schmitt 2002) and habitat quality (Krüger & Lindström 2001). Effects of these factors on movement rules are often inferred from a change in the observed distribution of individuals among habitats after a certain time interval, and as a result, these factors are treated as a ‘slope’ between habitats that makes it easier to go in one direction and more difficult to

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return. However, there is no *a priori* reason why such 'slope' is the correct representation, and it is possible that these factors modify the movement rules differently depending on the directions of the movement. Do these factors facilitate or inhibit habitat use by animals, or do they attract animals to or repulse animals from the certain habitats? Habitat-choice models have not incorporated these process-based movement rules because of the difficulty in quantifying them from pattern-based fitting of observed distributions.

The underlying rules for animal movement can be quantified from individual time series of habitat transitions by fitting a continuous-time Markov chain model. In this model, an individual at any given time is in one discrete state (habitat), and the time to move to the next state has a Markov property, a stochastic process in which a future state depends upon the current state (Bremaud 2001). This model allows us to quantify the likelihoods of transitions between each pair of states and investigates directional effects of additional factors. For example, Harcourt *et al.* (2009, 2010) applied this model to observed habitat transitions in pairs of sticklebacks and quantified the interplay of individual temperaments on leadership/followership in collective movement.

We used this approach to disentangle the effects of competitor size, behavioural interactions and habitat quality on movement rules of larval fish (red drum, *S. ocellatus*). Red drum spawn offshore and larvae are transferred to estuarine habitats by tidal currents (Brown *et al.* 2005). This non-territorial coastal fish is suitable for this study because size structure (about 7–25 mm standard length) and densities of larvae vary in the settlement habitats through the season as a result of batch spawning over many weeks (Rooker *et al.* 1998). Both large and small red drum larvae are found in the shallower (and thus, lighter) parts of seagrass beds, whereas only small larvae are found in the deeper (and thus, darker) areas (Pérez-Domínguez 2004), suggesting size-dependent habitat use, and possibly, competition over habitat use between different sizes. It is likely that smaller individuals are competitively inferior, considering that they receive more aggressive behaviour from larger individuals than vice versa (Nakayama, Ojanguren & Fuiman 2009) and that interference competition for food has a greater impact on smaller individuals (Nakayama & Fuiman 2010).

To evaluate the effects of the size of conspecifics and behavioural interactions on habitat use, we created a condition in a tank where larvae arrived to a habitat that was already occupied by a conspecific. A size-matched fish was used to simulate habitat competition between individuals from the same cohort, and a larger fish was used to simulate habitat competition with an individual from an earlier cohort. Also, to evaluate the effect of patch quality on movement rules, we simulated a temporal fluctuation of patch quality by adding food on one side of the tank. The time-series data of habitat transitions were fitted with a continuous-time Markov chain model to disentangle and evaluate the directional effects (i.e. facilitation, inhibition, attraction, repulsion) of the presence of a competitor, behavioural interactions and habitat quality.

Materials and methods

Six batches of red drum eggs were obtained from captive adults at the University of Texas Marine Science Institute (Port Aransas, TX, USA) on March 11, 15, 22, 23, 26 and 1 April 2009. Spawning was induced by manipulating photoperiod and water temperature. Eggs were spawned at about 20.00 h, collected at about 10.00 h the next day, treated with $5.0 \times 10^{-5}\%$ formalin in sea water for 30 min and put in 60-L fibreglass rearing tanks, at 5000 eggs per tank. Eggs hatched the same day. Larvae were fed once a day a mixture of rotifers (enriched with Algamac 2000; Aquafauna Bio-Marine, Inc., Hawthorn, CA, USA) and artificial diets (Otohime, Reed Mariculture, Inc., Campbell, CA, USA) from 1 to 10 days after hatching and enriched *Artemia* nauplii and artificial diets from 10 days after hatching and thereafter. Larvae were fed *ad libitum*. Water temperature and salinity were kept at 27.0 ± 0.3 °C (mean \pm SD) and 26.6 ± 0.8 p.p.t., respectively, for all tanks. Photoperiod was set at 12-h light and 12-h dark.

For experiments, we changed the light intensity in a glass aquarium (80 wide \times 15 cm deep) horizontally by one side of the tank being lit from above with a 150-W incandescent light bulb, and the other side covered with a black wooden board (Fig. 1). Light intensity was measured every 10 cm along the centre axis of the tank 5 cm below the water surface using a light sensor (LI-192 Underwater Quantum Sensor, Lincoln, NE, USA). We assumed that light attenuation was negligible through the 15-cm water depth. Three sides of the tank were covered with black paper to minimize visual distractions for the fish, and the front side was left uncovered for behavioural observations. A transparent Plexiglas partition was placed in the middle of the tank parallel to the front side of the tank to restrict the perspective depth to 15 cm. An aquarium heater was put behind the partition to maintain a constant temperature during trials.

At the age of 3–4 weeks old, 10 focal fish were randomly selected from the rearing tank 1 day before the experiment. Two to five fish of the same size (size-matched competitors) and two to five larger competitors were also selected 1 day before the experiment. Standard lengths of the fish we used in the experiments were 8.3 ± 0.1 mm for focal fish, 8.2 ± 0.1 mm for size-matched fish and 13.9 ± 0.2 mm for larger fish. Size-matched competitors were the same age as the focal fish, and larger competitors were 10–12 days older than the focal fish, which mimics the natural interval of successive cohorts arriving at the nursery habitats (Peters & McMichael 1987). Focal fish and the size-matched competitors were put individually into 100-mL plastic containers with food (50 *Artemia* nauplii), and the larger

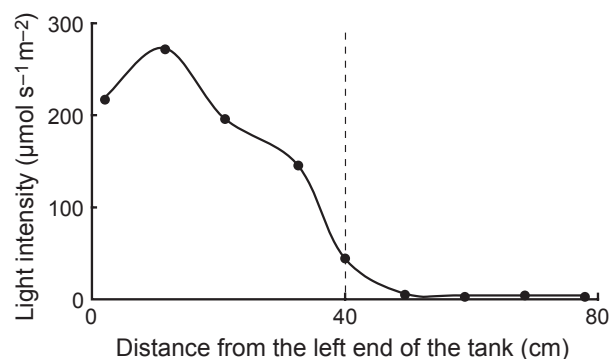


Fig. 1. Light intensity in the experiment tank. Dashed line marks the position of a habitat border between the light side and the dark side (the centre of the tank). Each point represents the mean value of three independent measurements.

competitors were put individually into 1-L plastic containers with food (200 *Artemia* nauplii).

The following day, each focal fish was randomly assigned to one of three treatments: (i) no competitor, (ii) with a size-matched competitor and (iii) with a larger competitor. Each trial began by placing the focal fish in a white PVC pipe (5 cm in diameter, 30 cm long) that stood vertically in the middle of the tank (40 cm from the left end of the tank), and then the competitor (except for the 'no competitor' treatment) was introduced on the light side of the tank. After 10 min of acclimatization, the pipe was gently lifted, and the focal fish was released into the tank to simulate the arrival of the focal fish to a settlement habitat that was already occupied by a conspecific. Two video cameras (Digital Handycam, DCR-TRV350; Sony Corp., Tokyo, Japan) were used to record behaviour from the front of the aquarium, with each camera recording one half of the tank. After 20 min of recording, food (50 *Artemia* nauplii) was gently put into the corner of the light side using a pipette, and the recording continued for 10 min. Food was added on the light side to increase the difference in habitat quality because our preliminary observations indicated that red drum larvae preferred the light habitat. Food stayed on the light side during this period because of the positive phototaxis and poor locomotor abilities of *Artemia*, and food was not depleted during the observation.

After the trial, focal fish were put back individually into 100-mL plastic containers with food (50 *Artemia*) overnight. The trials were conducted for three consecutive days for each individual, so that each fish was tested in all treatments. The treatment and the order of focal fish tested were randomized each day. Trials were conducted from 09.00 to 18.00 h. Water was changed after each experiment. Water temperature and salinity were 26.7 ± 0.5 °C and 27.1 ± 0.6 p.p.t., respectively. In total, three sets of the experiments were conducted (30 focal fish). We did not identify sex, as sexual characters do not develop at this early stage in red drum.

From the video recordings, we noted the time and type of behavioural interactions that occurred among red drum using event-recording software (JWATCHER v1.0, <http://www.jwatcher.ucla.edu>) by playing back the video at three times the real-time speed. Behavioural interactions were categorized as: aggressive behaviour by the focal fish, aggressive behaviour by the competitor and pre-attack escape behaviour by the focal fish. An aggressive behaviour was recorded when one fish chased the other fish from behind or attacked with rapid swimming speed. A pre-attack escape behaviour was recorded when a fish accelerated and swam away from the other fish without receiving an obvious aggressive display, which indicates vigilant propensity (Nakayama, Ojanguren & Fuiman 2009). It is possible that this behaviour was a response to an aggressive display by a competitor that the human observer could not detect. When two fish faced each other and swam away in opposite directions rapidly, a pre-attack escape behaviour was recorded for both fish. We also measured the timing of habitat transitions between the two habitats (light side and dark side) by focal fish and competitors. After the experiments, we euthanized the fish with an overdose of clove oil, took digital pictures through a dissecting microscope and measured their standard length using image analysis software (IMAGEJ v1.42, <http://rsbweb.nih.gov/ij/>).

STATISTICAL ANALYSIS

The time spent by focal fish on the light side (min per 10-min observation period) was compared among treatments (no competitor, size-matched competitor, and larger competitor) and between before and after food was introduced, using a repeated measures two-way ANOVA

with Bonferroni correction. The number of behavioural interactions observed during the trial was log-transformed after adding one and compared between competitor types (size-matched and larger competitors) using a paired *t*-test.

A continuous-time Markov chain model was used to analyse the intensity of habitat transition of focal fish (MSM v0.8 in R v2.9.0, <http://www.r-project.org>). As waiting time to the next state is exponentially distributed in this model, a rate parameter of the exponential distribution represents the transition intensity of the state (likelihood of habitat shift). Three factors were included in the models: competitor type (three levels: no competitor, size-matched competitor, larger competitor), the type of behavioural interactions between two competing fish (four levels: no interactions, aggressive behaviour performed, aggressive behaviour received, pre-attack escape behaviour) and the presence of food (two levels). In the model, each behavioural interaction began at the onset time of the behaviour and continued until the time of the next habitat transition or the next behaviour, whichever occurred first. Statistical interactions between the factors were omitted because the model failed to converge during the maximum likelihood estimation process, suggesting that the model with the interaction terms was overly complex for the observed data. To determine whether omitting any factors from the model would significantly decrease the model fit, we performed a likelihood ratio test, with a Chi-squared statistic equal to the difference in deviance between models, the degrees of freedom equals the difference in the parameters between models (Vanebles & Ripley 2002). As the model with all three factors turned out to be the best choice, we obtained the loglinear effects of the factors (competitor size, behavioural interactions, food) on transition intensities between habitats. In continuous-time Markov chain models, loglinear effects indicate how covariates change transition intensities compared with the model without covariates. To test whether a focal fish moved from light to dark more frequently than from dark to light, the ratios of transition intensities were computed by bootstrapping 1000 times to estimate statistical significance. A ratio significantly different from 1 indicates stronger transition intensity from one state to the other. The significance level (α) was set at 0.05 for all statistical tests. The descriptive statistics are reported as means \pm SE.

Results

When fish were alone without food, the time spent on the light side of the tank was significantly > 5 min (in 10 min of observation), the expected duration when habitat preference was not affected by the light condition ($t = 13.36$, d.f. = 29, $P < 0.001$; Fig. 2). The time spent by focal fish on the light side of the tank was significantly influenced by competitor type ($F_{2,58} = 7.03$, $P = 0.002$). When fish were alone, they spent 8.79 ± 0.22 min during a 10-min observation on the light side of the tank (an average of before and after adding food). When fish were with a size-matched fish, they spent a similar period on the light side (8.73 ± 0.22 min; paired *t*-test, $t = 0.21$, d.f. = 59, $P = 0.836$). However, focal fish spent significantly less time in the light habitat when they were with a larger fish (7.14 ± 0.38 min; paired *t*-test, $t = 3.74$, d.f. = 59, $P = 0.001$ after Bonferroni corrections). On average across treatments, focal fish spent 7.71 ± 0.22 min on the light side before food was added, which increased significantly after food was added on the light side of the tank (8.73 ± 0.26 min; $F_{1,29} = 17.25$, $P < 0.001$).

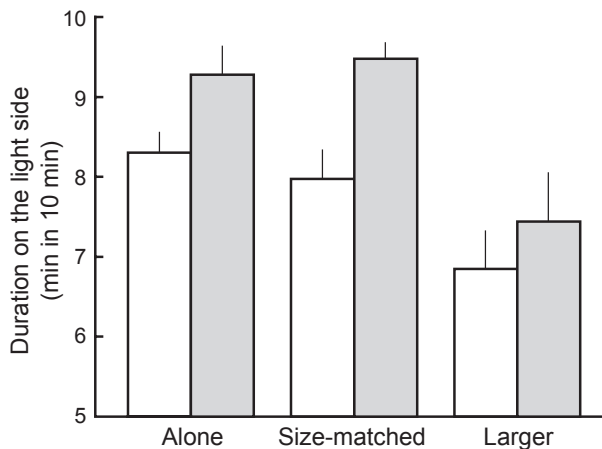


Fig. 2. Duration of focal individuals on the light side of the tank when they were alone, with a size-matched fish and with a larger fish (mean \pm SE, min in 10 min). Open bars indicate before food was added on the light side, and shaded bars indicate after food was added.

No significant interaction between competitor type and the presence of food was found ($F_{2,58} = 1.44$, $P = 0.245$).

Focal fish performed 0.10 ± 0.06 aggressive behaviours in 30 min to a size-matched fish but none to a larger fish. Focal fish received a greater number of aggressive behaviours from a larger competitor (1.20 ± 0.33) than a size-matched fish

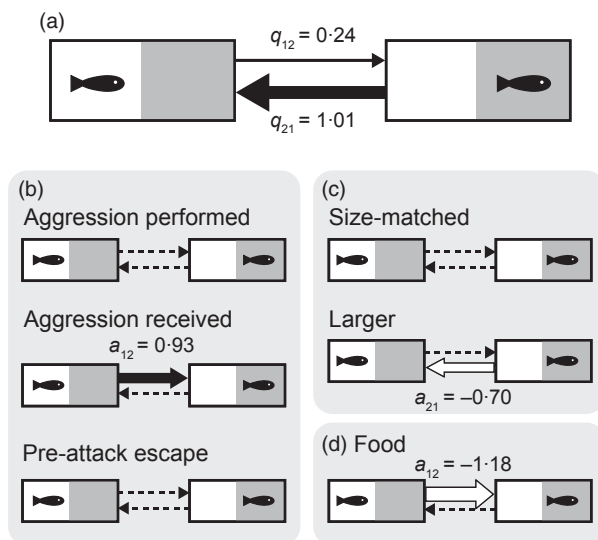


Fig. 3. Continuous-time Markov chain model with two-state transitions (light and dark). (a) Transition intensities from the light side to the dark side (q_{12}) and from the dark side to the light side (q_{21}) without covariates. (b) Loglinear effects of behavioural interactions. Top: effect of aggressive behaviour performed by focal individuals, middle: effect of aggressive behaviour received by focal individuals, bottom: pre-attack escape behaviour. (c) Loglinear effects of the presence of a conspecific. Top: effect of a size-matched fish, bottom: effect of a larger fish. (d) Loglinear effect of food. Widths of the arrows indicate magnitudes of transition. Black arrows indicate positive effects, and white arrows indicate negative effects. Dashed lines indicate no significant effect.

(0.20 ± 0.09 , $t = 3.21$, d.f. = 29, $P = 0.003$). The number of pre-attack escape behaviour was not different between the competitor types (with a size-matched fish: 1.97 ± 0.41 , with a larger fish: 2.30 ± 0.46 , $t = 0.52$, d.f. = 29, $P = 0.608$). No cannibalism was observed.

The Markov chain model without covariates (null model) showed that focal fish were four times more likely to shift from the dark side to the light side than to shift in the opposite direction ($q_{21}/q_{12} = 4.12 \pm 0.25$, $P < 0.001$, Fig. 3a). Including all covariates (competitor types, behavioural interactions and the presence of food) significantly improved the model fit ($\chi^2_{12} = 208.64$, $P < 0.001$). Omitting any covariates from the full model significantly decreased the model fit (likelihood ratio test, $P = 0.038$ against the model with behavioural interactions alone, $P < 0.001$ against all other alternative models). Aggressive behaviour received by focal fish significantly increased the transition intensity of focal fish from the light side to the dark side, whereas the other behaviours did not affect transition intensities (Fig. 3b). The presence of a size-matched fish did not affect transition intensities of focal individuals, whereas the presence of a larger fish significantly decreased the transition intensity of focal individuals from the dark side to the light side (Fig. 3c). The presence of food decreased the transition intensity of focal fish from the light side to the dark side, but it did not affect the transition intensity from the dark side to the light side (Fig. 3d).

Discussion

Our results demonstrate that the environmental factors do not simply act as a 'slope' between habitats that makes it easier to go in one direction and more difficult to return. Rather, these factors modify the movement rules differently depending on the directions of movement. Investigation of the transition intensities revealed that individuals were more likely to move from the dark side of the tank (called 'the poorer habitat' hereafter) to the light side (called 'the better habitat') than in the opposite direction (Fig. 3a). Individuals were less likely to enter the better habitat in the presence of a larger fish ('inhibition'), more likely to shift to the poorer habitat when they received aggressive behaviour ('repulsion') and more likely to stay in the better habitat when food was present in the better habitat ('facilitation'). However, no effect was found on the transition intensity for moving in the opposite direction. We argue that it is more appropriate to infer how animals assess the quality of a current habitat from the changes in habitat transition intensity (i.e. changes in movement rules) than from the overall change in habitat use per unit time (i.e. a change in habitat preference), because the latter can be observed either when individuals move out of a habitat more often or when individuals stay in a habitat longer. Disentangling the effects of environmental factors on movement rules would enhance habitat-choice models.

Our results confirm that aggressive interactions allow aggressive individuals to exploit good habitats by displacing competitors to poor habitats (Bay, Jones & McCormick 2001). The aggressors did not change their transition intensi-

ties between the habitats, indicating that they retained their preferred habitat use (Fig. 3b). On the other hand, the individuals that received aggressive behaviour were more likely to shift to the poorer habitat (i.e. repulsion), but the likelihood of abandoning the poorer habitat did not change during each visit. Receiving aggressive behaviour did not inhibit fish from entering the better habitat, probably because the occurrence of aggression indicates that hierarchy has not been established between the individuals. Although we did not observe cannibalism, aggressive behaviour may represent attempted predation rather than competition for habitat. In any case, we can infer that receiving aggressive behaviour from conspecifics decreases the perceived quality of the better habitat without changing the perceived quality of the poorer habitat.

The presence of a conspecific fish affected the movement rules differently depending on the fish size. In the presence of a size-matched fish, fish did not change their movement rules, indicating that there was no perceived change in habitat quality in either habitat (Fig. 3c). On the other hand, in the presence of a larger fish, fish were more likely to stay at the poorer habitat for a longer time during each visit (i.e. an increase in the perceived habitat quality of the poorer habitat), whereas the likelihood of abandoning the better habitat did not change during each visit (i.e. no change in perceived habitat quality of the better habitat). Our results help explaining the observed habitat use of red drum larvae in wild. Specifically, small red drum larvae occur in the deeper (and darker) periphery of seagrass beds, and both small and large larvae occur in the shallower (and lighter) centre of seagrass beds (Pérez-Domínguez 2004), consuming partially overlapping prey fields (Soto *et al.* 1998). Size-dependent habitat segregation is often assumed as a consequence of a decrease in perceived habitat quality of the preferred habitat through intraspecific competition (Bohlin 1977; Davey *et al.* 2005). In contrast, our results suggest that the presence of a larger fish does not decrease the perceived quality of a good habitat, but instead, it increases the perceived quality of a poor habitat.

From these results, being small is disadvantageous in competition over habitat for two different reasons: (i) small individuals are less likely to enter a better habitat in the presence of larger conspecifics and (ii) they would be more likely to abandon a better habitat, as they are more likely to receive aggressive behaviour from larger conspecifics (Nakayama, Ojanguren & Fuiman 2009). Identifying directional effects on movement rules is helpful in understanding the mechanisms of animal distribution and enhancing habitat-choice models, especially with IBM approaches, because the modification of movement rules change biologically relevant parameters, such as encounter rates with competitors and exploration duration of a habitat.

Addition of food increased the contrast in quality between the two habitats, and individuals were more likely to stay longer in the better habitat (Fig. 2). However, the transition intensity from the poorer habitat to the better habitat did not increase, indicating that there was no change in the perceived

quality of the poorer habitat, and they still spent the same amount of time exploring the poorer habitat during each visit (Fig. 3d). It is unlikely that fish in the poorer habitat simply could not detect the food in the better habitat, considering that fish were swimming constantly between the habitats in a relatively small tank. Although individuals can also spend more time in the better habitat by increasing the transition intensity from the poorer habitat to the better habitat, this results in more frequent trips between the habitats. It would be disadvantageous if travelling between habitats increases predation risk or is energetically costly (Stamps, Krishnan & Reid 2005). Therefore, the observed change in habitat transition after food was added could be an adaptive response to simultaneously increase the time staying in the better habitat and decrease the frequency of habitat transition, which still allows individuals to explore the poorer habitat for the same amount of time during each visit.

In red drum larvae, smaller individuals exhibit pre-attack escape behaviour more often than larger individuals (Nakayama, Ojanguren & Fuiman 2009). This behaviour decreases feeding activity through interference competition for food (Nakayama & Fuiman 2010), and therefore, it can be considered as vigilance to conspecifics. Similarly, vigilant behaviour to predators is often associated with decreased foraging time (Brown 1999; Watson, Aebischer & Cresswell 2007). However, lack of an effect of pre-attack escape behaviour on habitat transition intensity suggests that interference competition for habitat use operates differently from interference competition for food. Alternatively, the costs of this behaviour may be simply balanced by the benefits of staying close to conspecifics, such as a reduced predation risk (Brown & Warburton 1999) and increased probability of finding food (Dugatkin & Alfieri 1991), resulting in no change in the observed intensity of habitat transition.

We conclude that directional effects (i.e. facilitation, inhibition, attraction, repulsion) can have an important influence on movement rules in response to different environmental factors. Effects of environmental factors on habitat choice are confounded by the interplay of different directional effects (i.e. processes) if we simply look at the patterns of animal distribution. Continuous-time Markov chain models allow us to evaluate quantitatively the effects of environmental factors on transition intensities on both directions of movement. This process-based approach is applicable in more complex systems, such as prey–predator interactions and species invasions when the time-series data are available. Process-based movement rules at the individual level will contribute to models of animal distributions at the population level, which are crucial for understanding community structure and evolutionary processes.

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