

TESTS OF THEORY FOR DIEL VARIATION IN SALMONID FEEDING ACTIVITY AND HABITAT USE

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Abstract. For many animals, selecting whether to forage during day or night is a critical fitness problem: at night, predation risks are lower but feeding is less efficient. Habitat selection is a closely related problem: the best location for nocturnal foraging could be too risky during daytime, and habitat that is safe and profitable in daytime may be unprofitable at night. We pose a theory that assumes animals select the combination of daytime and night activity (feeding vs. hiding), and habitat, that maximizes expected future fitness. Expected fitness is approximated as the predicted probability of surviving starvation and predation over a future time horizon, multiplied by a function representing the fitness benefits of growth. The theory's usefulness and generality were tested using pattern-oriented analysis of an individual-based model (IBM) of stream salmonids and the extensive literature on observed diel behavior patterns of these animals. Simulation experiments showed that the IBM reproduces eight diverse patterns observed in real populations. (1) Diel activity (whether foraging occurs during day and/or night) varies among a population's individuals, and from day to day for each individual. (2) Salmonids feed in shallower and slower water at night. (3) Individuals pack more tightly into the best habitat when feeding at night. (4) Salmonids feed relatively more at night if temperatures (and, therefore, metabolic demands) are low. (5) Daytime feeding is more common for life stages in which potential fitness increases more rapidly with growth. (6) Competition for feeding or hiding sites can shift foraging between day and night. (7) Daytime feeding is more common when food availability is low. (8) Diel activity patterns are affected by the availability of good habitat for feeding or hiding. We can explain many patterns of variation in diel foraging behavior without assuming that populations or individuals vary in how inherently nocturnal or diurnal they are. Instead, these patterns can emerge from the search by individuals for good trade-offs between growth and survival under different habitat and competitive conditions.

Key words: diel activity; diurnal; foraging; habitat selection; individual-based model; nocturnal; salmonid; theory.

INTRODUCTION

Understanding diel patterns of habitat selection and activity is a particularly challenging ecological problem. Some species are clearly specialized for either diurnal or nocturnal foraging, but for other animals choosing whether to forage during day or night is a critical decision. During the day, food is generally easier to detect but predation risk is often higher (Metcalf et al. 1999). Habitat selection is a closely related behavior because the value of a habitat for feeding or hiding differs between day and night. Habitat that provides a good trade-off between energy intake and mortality risk during the day might be unprofitable for nocturnal foraging, and habitat highly profitable for nocturnal foraging might be too risky during daytime.

Stream-dwelling salmonids, for example, exhibit complex and variable diel activity patterns (Reebs 2002). Summer observations have often found most, but not all, salmonids feeding during the day and hiding at night (e.g., Young et al. 1997, Bradford and Higgins 2001). Bremset (2000) and Cunjak et al. (1998) observed juvenile Atlantic salmon (*Salmo salar*) generally shifting to nocturnal feeding and diurnal hiding during cold seasons, but there were many exceptions to this generality. Nocturnal feeding in winter is often attributed to reduced metabolic needs and higher predation risk at low temperature (Bull et al. 1996, Heggenes et al. 1999, Jakober et al. 2000). However, Amundsen et al. (2000) observed nocturnal feeding in Atlantic salmon during August and September, which they attributed to seasonal changes in food availability. Nocturnal feeding has been shown to be more prevalent among larger fish in some cases (e.g., Metcalfe et al. 1998, Amundsen et al. 1999) but not in others (e.g., Gries and Juanes 1998). Interactions between activity

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and habitat selection are illustrated by observations that salmonids use different habitat for feeding vs. hiding (Heggenes et al. 1999, Hiscock et al. 2002), and that diel activity patterns vary with reach-scale habitat features (Bradford and Higgins 2001). Metcalfe et al. (1999), after a series of controlled laboratory experiments on stream-dwelling juvenile salmon, drew this conclusion:

Daily activity patterns are therefore suggested to be the result of a complex tradeoff between growth and survival, which takes account of diel fluctuations in food availability, food capture efficiency and predation risk; individual variation in the extent of diurnal feeding in salmon may result from state-dependent differences in the benefits of rapid feeding and growth.

We present and test a general theory for how individual animals make this complex trade-off between growth and survival to select nocturnal and diurnal activity and, in conjunction, their microhabitat. To test the theory, we implemented it in an individual-based model (IBM) of stream-dwelling salmonids in a realistically complex context: growth potential and mortality risks vary over space and time, among individuals, between day and night, and between feeding and hiding activity; and individuals compete with each other for food and cover for hiding and feeding. The theory is an extension of the state-based, predictive, fitness-maximization approach to decision-making (Railsback et al. 1999), which modifies the dynamic state variable theory (Houston and McNamara 1999, Clark and Mangel 2000) by assuming animals use simple predictions to estimate their potential fitness over a future time horizon. For convenience, we refer to the theory investigated here as SPHAST (state-based, predictive habitat- and activity-selection theory). SPHAST comprises two major assumptions:

1) Individual animals select the combination of diurnal and nocturnal habitat and activity that maximizes their expected fitness over a future time horizon. (This time horizon is not the decision time step: individuals repeat their habitat and activity choice at a half-day time step, the start of each day and night, while considering its consequences over the much longer time horizon.) When individuals decide which activity to perform, they consider the consequences of both day and night activities, not just the activity selected for the current time; and they consider the best available habitat (within the area the animal is familiar with) for each activity. We do not necessarily assume the individuals carry out complicated optimizations, but instead assume they have evolved or learned fitness-seeking behaviors that are usefully approximated as optimizations.

2) An individual's expected fitness, for some combination of habitat and activity, is approximated by a measure (which we refer to as EF) that has two terms.

First is the probability of surviving both starvation and predation risks over a future time horizon (90 d, in this study). The second term is the individual's size at the end of the time horizon, relative to two "landmarks": the minimum size for reproduction and the size of the largest competing animal. This term represents the importance of growth to fitness. Thus, EF depends on the individual's current physiological state and a simple projection of growth and mortality risks over the time horizon. This approximation of future fitness is especially useful for individuals not in the reproductive cycle (e.g., juveniles) because it does not explicitly represent reproduction; instead, it is assumed that eventual reproductive success is usefully approximated by the survival probability and growth rate over the upcoming 90 days.

Under these two assumptions, an individual's diel activity pattern depends on habitat availability, the individual's state, and the ways in which habitat conditions and activity affect the individual's growth and survival. The choice of activity and habitat during one diel phase (day or night) depends on expected choice of activity and habitat during the opposite phase. For example, the availability of good habitat for nocturnal feeding could result in diurnal hiding.

The second of these two assumptions was tested successfully by Railsback and Harvey (2002), who applied it to daytime habitat selection in stream-dwelling salmonids. When their IBM assumed that fish select habitat to maximize a term similar to EF, it reproduced a wide variety of observed habitat selection behaviors that were not all reproduced when alternative habitat selection theories were assumed.

Here we focus on SPHAST's first assumption, testing whether it is capable of reproducing a variety of observed behaviors. To test the theory, we employ pattern-oriented analysis using individual-based simulation (Railsback 2001, Railsback and Harvey 2002). We (1) implemented SPHAST in a stream trout IBM that includes many natural habitat complexities, (2) identified eight patterns of diel activity and habitat selection observed under known conditions, (3) simulated those conditions in the IBM, and (4) determined how well the observed patterns were reproduced by the IBM. If the IBM reproduces a wide range of observed patterns, the simulation experiments support the assumption that SPHAST is a useful, general model of activity and habitat selection.

SPHAST is posed as a general theory or model of how diel selection of activity and habitat by individuals is affected by spatial and temporal variation in growth potential, mortality risk, and individual state. While we focus here on stream salmonids, SPHAST should also be equally useful in modeling the activity and habitat selection of other animals with variable diel patterns of behavior (e.g., deer, Kilgo et al. 1998; rodents, Kotler et al. 2004). In fact, the theory potentially could be applied to taxa exhibiting less variable patterns, such

TABLE 1. Initial trout population characteristics.

Age (yr)	No.	Length (cm)	
		Mean	1 SD
1	50	12	0.8
2	50	25	2.0
3+	250	40	3.0

as the strong yet sometimes unexplained patterns in diel foraging behavior and habitat selection observed in tropical fish (Arrington and Winemiller 2003).

METHODS

Study site and simulated conditions

This study is based on simulation experiments using an IBM applied to the Pipe Creek reach of the Green River, 3 km below Flaming Gorge Dam, Daggett County, Utah, USA. This site supports dense populations of large rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), which subsist almost entirely on benthic macroinvertebrates (Filbert and Hawkins 1995). Habitat input was developed from data collected at 10 transects by the U.S. Fish and Wildlife Service in 1987 (Hann et al. 1991). These transects averaged 104 m in width and included a variety of habitat types: a riffle; a deep, fast chute; and a pool with both deep and shallow areas. To provide realistic trout densities without unwieldy numbers of individuals, we assumed each transect represented only 3 m of river length. The model's habitat cells were also typically 3 m in across-channel width. A hydraulic model was used to estimate depth and velocity in each cell. The availability of hiding and feeding cover in each cell was estimated from field observations we made in October 2001.

We defined a baseline scenario for simulation experiments. The baseline scenario ran from 1 May to 31 August, but to assure that results were not unduly affected by initial conditions (e.g., fish were initialized with healthy mass for their length and, therefore, minimal risk of starvation) we only analyzed results from the last seven days of each simulation. Flow was held constant at a typical summer value of 60 m³/s. At this flow the model included 173 cells covering 1556 m². Water velocities varied among cells from 3 to 193 cm/s with a mean of 65 cm/s; cell depth varied from 5 to 643 cm with a mean of 180 cm. Daily water temperature input was from values measured in 2001, and ranged from 7° to 12°C.

To simplify the analysis, the trout community was simulated as a single species having an abundance and age structure typical of the study site's entire trout assemblage. The total trout biomass was estimated as the mean of densities reported for two sites a few kilometers upstream (840 kg/ha) and downstream (500 kg/ha) of our site (Filbert and Hawkins 1995). The assumed initial abundance and mean length of each age class (Table 1) were determined, in part, from field data

collected just downstream of Flaming Gorge Dam in 1997–1999 (S. Brayton, *unpublished data*). The age structure of this trout population is unusually weighted toward large, old fish, a result of stocking hatchery trout, high secondary production, and habitat that is better for large than small trout (Johnson et al. 1987). To simplify our simulation experiments, we used only three age classes: 1, 2, and 3 and higher (3+) years; we also ignored recruitment of new trout via spawning or stocking.

Individual-based salmonid model

Overview.—To test the activity and habitat selection theory in a realistically complex context, we used the trout IBM described in detail by Railsback and Harvey (2001, 2002) and summarized in the following three paragraphs. Modifications of the IBM for this study are described afterward, starting at *Methods: Diel variation*.

The IBM simulates stream habitat as a mosaic of rectangular cells. Habitat characteristics (e.g., depth, velocity, distance to hiding cover) vary among cells. Cell depth and velocity depend on the simulated flow rate (m³/s) which, along with temperature, varies daily.

Trout growth is modeled as a function of food availability, the trout's ability to catch food, competition among trout, and metabolic energy costs. The IBM assumes feeding is only on macroinvertebrates because (1) piscivory by trout appears to be rare at the study site (Filbert and Hawkins 1995), and (2) the observations against which we compare simulation results (see *Results*) were all of small fish that can safely be assumed to eat macroinvertebrates. Two separate feeding behaviors are simulated: search feeding (searching for stationary food such as invertebrates eaten off the river bottom) and drift feeding (holding a position and catching invertebrates as they drift past in the river flow). The availability of drifting food increases with both velocity and depth, but the reactive distance over which a fish can detect and capture drifting food decreases as velocity increases. Metabolic costs increase with swimming speed, which is assumed to equal the velocity of the cell where fish are feeding; however, drift-feeding trout that have access to velocity shelter have swimming costs reduced by 50%. The outcome of these processes is that simulated growth rate increases with velocity up to a peak velocity, after which growth declines. This peak velocity increases with trout size and is higher for trout using velocity shelters. The IBM assumes trout compete for food and velocity shelters via a size-based hierarchy. There is a fixed amount of food available per day in each cell and the food consumed by larger fish is not available to smaller fish. Metabolic costs, and therefore the food intake needed to avoid starvation, increase with temperature.

Risks are explicitly simulated for several kinds of mortality, the most important of which are predation by endothermic terrestrial animals and starvation. The

daily probability of surviving each kind of mortality is a function of habitat and fish conditions. Mortality risk from terrestrial predators—at our site, especially otters (*Lutra canadensis*), mergansers (*Mergus* spp.), bald eagles (*Haliaeetus leucocephalus*), and ospreys (*Pandion haliaetus*)—decreases with increasing depth and velocity; these factors make fish more difficult to see. Risk from terrestrial predators also decreases as the cell's variable representing distance to hiding cover decreases. The IBM does not assume that mortality from terrestrial predators is higher at cold temperatures; trout are less able to escape from warm-blooded predators when temperature is low (Metcalf et al. 1999) but many predators at our study site exhibit reduced activity in winter. Starvation risk is a function of a fish's mass compared to the mass of "healthy" fish of the same length; risk of starvation increases as mass declines during periods of negative growth.

Diel variation in feeding ability and predation risks.—We modified the IBM of Railsback and Harvey (2001, 2002) to represent differences between day and night in feeding ability and predation risks. For the drift-feeding strategy, in which trout detect prey entirely by vision, we assumed that the reactive distance over which trout can capture food is reduced by 50% at night. Food intake is related to the square of reactive distance, so intake at night is reduced to as little as 25% of daytime intake. This assumption is within the range of night feeding efficiencies (<35% of daytime) estimated by Fraser and Metcalfe (1997); Schmidt and O'Brien (1982), however, measured night reactive distances of a salmonid (arctic grayling, *Thymallus arcticus*) to be ~20–30% of daytime values. For the search-feeding strategy, we assumed food intake is reduced by 50% at night due to reduced vision. One reason for these relatively generous assumptions for night feeding was to keep simulated growth from being extremely sensitive to the assumptions; with a 50% reduction in reactive distance, all trout could obtain slightly positive growth under at least some habitat conditions. A second reason is because we did not explicitly represent the higher nighttime densities of drifting aquatic insects often cited as a contributor to diel variation in growth potential. We did not include diel variation in drift because it is site dependent and not always strong (Heggenes et al. 1993, Metcalfe et al. 1999), and because it would complicate the analysis.

We assumed the mortality risk due to terrestrial predators is 70% lower at night. Metcalfe et al. (1999) estimated a much higher diel difference in risk for juvenile salmonids in winter, for a river in Scotland. Our assumption of a lesser diel difference is based in part on our informal observation that otters, which hunt at least partly at night, are important predators at the site.

Variation in feeding and risks due to activity.—We also modified the IBM to represent hiding as an activity alternative to feeding. If a model trout chooses to hide instead of feed, its food intake and swimming speeds

are assumed to be zero so its growth is slightly negative. The IBM also represents competition among trout for a limited amount of hiding cover (e.g., Armstrong and Griffiths 2001). A model trout that chooses hiding activity has a strong incentive to select a habitat cell in which hiding cover is available: the risk of predation is reduced by 99% if a trout is using hiding cover because even adult trout hiding in cover have proven very difficult to detect (Jakober et al. 2000, Meyer and Gregory 2000). If no hiding cover is available in a cell, a model trout can still choose to exhibit hiding behavior but it will obtain no reduction in predation risk.

Hiding cover is represented as the fraction of cell area that provides hiding places, among rocks or in vegetation. To avoid additional complexity, the effect of fish size on availability of hiding places is not represented. Each hiding trout is assumed to use up an area of hiding cover equal to the square of its length. Access to hiding (like food and velocity shelters, the other two contested resources in the IBM) is allocated via sized-based competition: the largest trout are given first access to hiding cover and cannot be displaced by smaller trout.

Modeling activity and habitat selection with SPHAST.—The two fundamental assumptions of SPHAST were implemented with the following detailed steps.

- 1) Each 24-h day is separated into two phases: daytime and night. The daytime phase lasts from a half-hour before sunrise to a half-hour after sunset. During each phase, a fish either feeds or hides. The selected activity is performed for the entire phase, an assumption that simplifies the model and is supported by Metcalfe et al. (1999), who observed in a laboratory study that juvenile salmon usually exhibited one activity for the vast majority of a phase. Dawn and dusk may be important as short periods when light levels are low enough to reduce predation risks yet high enough for efficient foraging (Alanärä et al. 2001, Bradford and Higgins 2001). Dawn and dusk could be added to our model as separate phases with feeding and risk conditions differing from both night and daytime, but we chose to avoid this additional complexity, as did the laboratory studies we compare our model to.

- 2) The model executes activity and habitat selection simulations at the start of each daytime and night phase, so fish reevaluate their choice of habitat and diel activity pattern considering the conditions present at the start of each phase.

- 3) At the start of each phase, each fish identifies the habitat cells that are potential movement destinations: all cells within a radius within which fish are assumed familiar with their habitat. This assumption was based on field observations indicating that stream trout commonly "commute" 10s to 100s of meters to feeding sites and back each day (Gowan and Fausch 1996, Bunnell et al. 1998, Harvey et al. 1999). The radius for

potential destination cells increases with the square of the fish's length, reflecting the greater mobility of larger fish. Each model fish conducts steps 4–6 for each potential destination cell.

4) The fish determines the growth rate (g , g/h) and survival probability (S , probability of surviving for one day) it would experience in the cell during that phase, with separate values of g and S for the two activities: feeding and hiding. The values of g and S vary (in ways outlined previously and explained fully by Railsback and Harvey 2001) with habitat conditions (e.g., depth, velocity, temperature, availability of food and cover), the fish's state (e.g., length and mass), competition (consumption of food and cover by larger fish), and the phase (day vs. night). A number of studies (e.g., Bull et al. 1996, Grand and Dill 1997) have indicated awareness by salmonids of growth and risk conditions and the ability to adapt behavior to these conditions.

5) As an estimate of g and S during future phases, the fish uses memory of the best available g and S from the previous phase. For example, at the start of a night phase, the fish assumes that the growth and survival it will experience if feeding during future daytime phases are equal to the g and S it found, during the previous daytime, for the best habitat cell for feeding evaluated by the fish during the previous daytime. This memory approach is used because we cannot assume a fish uses the same cell for both daytime and night, and it is unrealistically difficult for a fish to forecast g and S in the following phase (e.g., the next night, if it is currently daytime) because such a forecast would require predicting what habitat and activity all larger fish would select. Previous empirical and simulation research supports the use of memory in modeling foraging decisions by fish (Milinski 1994, Hirvonen et al. 1999).

6) Using the values of g and S determined for the current phase and “remembered” from the previous phase, the fish calculates the value of EF it would obtain in the cell for each of the four possible activity combinations: daytime and night feeding, daytime feeding and night hiding, daytime hiding and night feeding, and daytime hiding and night hiding. Daily growth is equal to (g for daytime multiplied by the number of daytime hours) plus (g for night multiplied by the number of night hours). The daily survival probability is the average of S for daytime and night, weighted by the number of hours in each phase (equivalent to calculating hourly survival probabilities and the probability of surviving all 24 hours). Daily growth and survival are used to project the probability of surviving both starvation and other risks over a 90-d time horizon, by simply assuming that current growth rates and survival probabilities persist over the time horizon. This prediction of future survival is obviously simplistic (e.g., neglecting the effects of growth as well as habitat changes over the time horizon) but it has proven useful for modeling how animals make complex

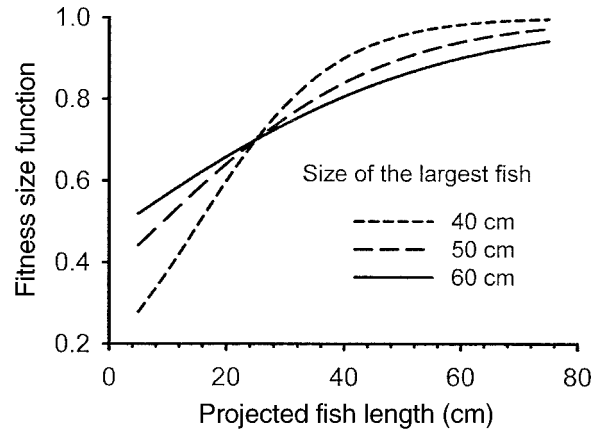


FIG. 1. Function for how expected fitness increases with fish length (a fish's projected length at the end of a 90-d time horizon). The three lines show the fitness size function when the largest fish is 40, 50, or 60 cm in length.

decisions (Railsback et al. 1999, Railsback and Harvey 2002).

EF is calculated by multiplying expected survival over the time horizon by a function representing the effect of fish size on fitness. This fitness size function represents how EF varies with the length the fish would achieve at the end of the 90-d time horizon, for the habitat cell and activity combination the fish is considering. Railsback et al. (1999) and Railsback and Harvey (2002) used a “fraction of reproductive maturity” function, which assumed that EF increases with size only until a fish reaches the minimum size needed for reproduction. However, when we gave model trout the choice of feeding vs. hiding it became necessary to represent how fitness continues to increase with length even after reproductive size is reached; otherwise, fish that reach reproductive size would stop growing and feed only enough to avoid starvation. In reality, salmonids continue to grow well beyond the minimum size of reproduction. Reaching reproductive status is a major fitness milestone, but for salmonids fitness is very likely to increase with further growth. Larger fish produce more and larger eggs (Meyer et al. 2003), can bury eggs deeper in the substrate where the eggs are more likely to survive (DeVries 1997), and can out-compete other fish for habitat (Hughes 1992). Considering these factors, we assumed a fitness size function that is a function of fish length, L . The function (Fig. 1) is a logistic curve defined by two points. It equals 0.7 at the minimum length needed for reproduction (assumed to be 25 cm for the study site) and equals 0.9 at the length of the largest fish in the population (L_{\max}):

$$FSF = \frac{\exp(Z)}{\exp(1 + Z)} \quad (1)$$

where

$$Z = A + (L \times B)$$

$$A = -\frac{0.503}{(25 - L_{\max})}$$

$$B = -0.251 - (25A).$$

7) After considering all potential destination cells, the fish identifies the cell providing the highest EF for any of the four activity combinations. This cell is selected as the fish's new habitat, and it selects the activity providing the highest EF. For example, if the combination of daytime hiding and night feeding provides highest EF in the best cell, and it is currently the start of daytime, then the fish's selected activity is to hide.

Software.—The complexity of IBMs demands special attention to software (Ropella et al. 2002). We implemented the IBM using the Swarm simulation system (Minar et al. 1996), which provides graphical observation tools enabling us to see and check habitat simulations and behavior of individual fish. We then tested the software extensively because mistakes are unlikely to be apparent from model results alone. Intermediate results from the IBM's key "submodels" were output and compared to results from the same submodels implemented independently in spreadsheet software. This technique tested the trout's decision-making code for many thousands of cases under a wide variety of conditions.

Calibration.—To keep from biasing the analyses, we did not undertake a detailed calibration of the IBM. All parameter values were taken from the literature or determined via testing and calibration of each submodel (Railsback and Harvey 2001, 2002), with the following exceptions. The parameters controlling production of food were adopted from calibration of the model to another study site (Railsback and Harvey 2001); however, the parameter representing the stream length required for drift consumption to be replenished was halved to reflect the high productivity of the Green River site. Parameters for the fish size function of EF were tested by ensuring that the IBM reproduced four very basic patterns: (1) trout continue to grow indefinitely; (2) after reaching reproductive size, trout do not assume substantial mortality risks in order to grow; (3) the trout size distribution (mean mass for each age) is stable over a number of years; and (4) there is at least some feeding during both day and night.

Pattern-oriented analysis

Pattern-oriented analysis using an IBM is a practical yet comprehensive way to test theories for how population-level patterns emerge from individual behavior (Railsback 2001, Railsback and Harvey 2002, Grimm and Berger 2003, Grimm and Railsback 2005). Theories are tested by implementing them in IBMs and determining how well they reproduce a variety of observed patterns, referred to as test patterns. By using

test patterns observed at both the individual and population levels, we can identify theories that explain both individual behavior and the population-level responses that emerge from individual behavior. A priori, we identified eight test patterns of diel activity and habitat selection, many from the extensive laboratory and field experiments (cited below) of N. B. Metcalfe, N. H. C. Fraser, and colleagues at the University of Glasgow. Using the IBM, we reproduced the conditions under which the test patterns were observed, then observed whether IBM results reproduced the patterns. The design of each simulation experiment is described, along with its results (see *Results*).

This analysis used a wide range of qualitative test patterns instead of testing the IBM's ability to precisely reproduce a few quantitative patterns. Because (as our simulation experiments show) patterns of diel activity and habitat selection vary with many characteristics of the habitat and fish population, precisely reproducing observed results would require careful recalibration of the IBM for each scenario. Instead, we focus on testing how general SPHAST is by examining how well the theory reproduces qualitative responses to a wide variety of factors (Railsback 2001). However, we do state each test pattern as a specific criterion that the IBM was tested against.

Statistical comparisons

Two-sample *t* tests were used to determine the statistical significance of differences between simulation scenarios. We used five replicate simulations of each scenario to represent the variability that results from the IBM's stochastic elements. Results for all fish were averaged over the 7-d analysis period to produce one population-level mean value per replicate.

RESULTS

For each simulation experiment, we describe the test pattern, the conditions under which it has been observed in real salmonids, and how these conditions were simulated in the IBM. Then we present simulation results illustrating the extent to which the test pattern was reproduced. To avoid confusion between observations of real vs. simulated fish, the term "v-fish" is used for virtual fish in the IBM.

Pattern 1: Individual variation in diel activity

Diel activity patterns appear not to be uniform behaviors but instead to be general trends with variation among individual salmonids; individuals also are not strictly diurnal or nocturnal. For example, Young et al. (1997) found 100% of trout active in day during summer, but an average of one-third were also active at night; Gries and Juanes (1998) observed juvenile Atlantic salmon in summer and found 55% of age 0 salmon feeding during daytime. Therefore, the first test pattern is that diel activity selection varies among individuals of an age class, and over time for each indi-

TABLE 2. Percentage of fish feeding during day and night in the baseline scenario.

Age (yr)	Percentage of fish feeding	
	Day	Night
1	100	0
2	20	1
3+	12	48

Note: Percentage of fish feeding in day and percentage feeding in night do not sum to 100 because fish may feed during both day and night, or may not feed at all on some days.

vidual. To test whether SPHAST reproduces this pattern, we simply identified the percentage of v-fish feeding during day vs. night in our baseline scenario (Table 2). We also randomly selected three v-fish of each age class and observed their activity during the baseline scenario.

The pattern of individual variation was clearly reproduced for age 3+ v-fish: some (but not all) fed during day and some (but not all) fed during night. Further, the three individual v-fish we observed behaved differently. The largest v-fish of the three consistently fed every night, but the other two fed only occasionally (sometimes in day and sometimes at night) then hid for several days.

Age 2 v-fish had more consistent behavior, feeding almost exclusively during the day. About 20% of age 2 v-fish fed each day, but different individuals fed each day: each v-fish fed only on occasional days, averaging one day in five. The three individual v-fish we observed in detail displayed no night feeding.

Age 1 v-fish did not follow this test pattern in the baseline scenario: all individuals used the same behavior, feeding every day and hiding every night. However, results of other simulation experiments (for patterns 4, 7, and 8) show individual variation in age 1 activity when temperature, food availability, or habitat conditions are different than in the baseline scenario. Even in the baseline scenario, activity of age 1 v-fish varied during times preceding the final 7-d period reported in Table 2.

Pattern 2: Use of shallower and slower habitat for nocturnal feeding

This test pattern is that salmonids use habitat with lower depths and velocities for night feeding than daytime feeding, as observed by Harwood et al. (2001), Jakober et al. (2000), and Valdimarsson and Metcalfe (1999). One explanation for this habitat shift is that both low light levels and high velocity reduce the ability of fish to detect and capture prey; night feeding is therefore only efficient at lower velocities, which tend to occur along stream margins where depth is also low. Also, the risk from terrestrial predators in shallow, quiet habitat (where fish are easily seen from above or from shore) is less at night.

To determine if this pattern is reproduced by SPHAST, we contrasted the habitat used by adult v-fish that were active in daytime vs. night in the baseline scenario. We examined only age 3+ v-fish to avoid the confounding effects of competition for feeding and hiding space.

The IBM reproduced this test pattern: the mean depth used by v-fish feeding at night was 228 cm, compared to 299 cm for v-fish feeding in daytime ($P < 0.0001$). The difference in mean velocity between v-fish feeding at night (54 cm/s) and in day (56 cm/s) was small but statistically significant ($P = 0.018$). This difference in velocity may be small in part because night-feeding v-fish were larger (mean individual mass of 872 g, vs. 796 g for day-feeding individuals), and larger v-fish can feed productively at higher velocities than can smaller v-fish. The size difference between day- and night-feeding v-fish likely offsets the effects of light level on velocity use to some extent.

Pattern 3: Higher densities in preferred habitat at night

Valdimarsson and Metcalfe (2001) observed nocturnal Atlantic salmon displaying less aggression and consequently occurring at higher local densities than during daytime. A likely explanation is simply that the distances over which fish can feed are reduced at night, so there is no benefit to defending a larger territory. Therefore, this test pattern is that local densities of trout are higher at night. To test the ability of SPHAST to reproduce this pattern, we contrasted the density of feeding v-fish (in occupied habitat cells) between day and night, in the baseline scenario. We examined only age 3+ v-fish because very few younger v-fish fed at night.

The IBM also reproduced this test pattern. At night, the average density of feeding v-fish in occupied habitat cells was 0.28 individuals/m², compared to 0.17 individuals/m² in day ($P < 0.0001$).

Pattern 4: Less nocturnal feeding at high temperatures

An inverse relationship between temperature and the relative frequency of night feeding by salmonids has been observed by Bradford and Higgins (2001), Fraser et al. (1995), Gries et al. (1997), and Meyer and Gregory (2000). Mechanisms cited by these authors as potentially contributing to this relationship include: (1) reduced metabolic needs at low temperatures, reducing the need to feed during the day when risks are higher; (2) higher daytime predation risks at cold temperatures (fish swimming performance is worse at low temperatures, making fish less able to escape from warm-blooded predators); and (3) longer nights in winter that allow more nocturnal food intake. Fraser et al. (1995) conducted a laboratory experiment with juvenile Atlantic salmon, varying temperature over a 100-d period and observing how many fish fed during each day and

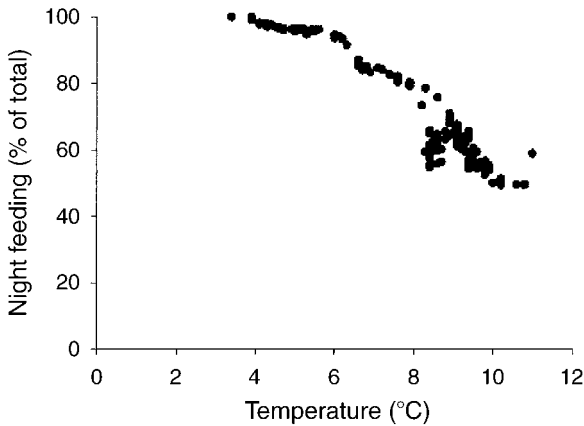


FIG. 2. Percentage of total v-fish (virtual fish) feeding that occurs at night, in relation to temperature. Each point represents one day in a single simulation of the period 25 August through 28 February. Values are the number of v-fish feeding at night, divided by the sum of the number of v-fish feeding during daytime and the number feeding at night.

night. Nearly 100% of the feeding occurred at night when temperature was around 5°C, and as temperature increased to 10°C the percentage of feeding that occurred at night dropped to around 50%.

The test pattern is that the relative frequency of nocturnal feeding decreases as temperature increases. We tested the ability of SPHAST to reproduce this pattern by using simulations that continued from our baseline period of late August through the following February, when temperatures are as low as 4°C. To match the experiment of Fraser et al. (1995), we (1) held day length constant, (2) assumed no effect of temperature on mortality from terrestrial predators or food availability, and (3) examined results in terms of percentage feeding that occurs at night (for each day, the number of v-fish feeding at night was divided by the sum of the number feeding during day plus the number feeding at night).

Simulation results closely matched those of Fraser et al. (1995), with the percentage of feeding that occurs at night dropping from near 100% to around 50% as temperature increased from 5° to 10°C (Fig. 2). This close match may be partly coincidental, as we simulated large adult v-fish in diverse habitat while Fraser et al. (1995) observed juveniles in laboratory conditions. Fraser et al. observed that nearly all fish fed every night under all temperatures, while the percentage of fish that fed during daytime and night increased with temperature. In our simulations the percentage of v-fish feeding on any one night decreased with temperature (perhaps because adults have less incentive to grow than juveniles; see *Results: Pattern 5*). In our results, reduced metabolism (the only effect of temperature in this simulation experiment) is sufficient to explain why feeding is often more nocturnal in winter.

Pattern 5: Effects of life history stage on activity pattern

Adult salmonids have been observed to feed less often in day than do juveniles (e.g., Gries and Juanes 1998, Bradford and Higgins 2001). One explanation of this pattern is the inability of juveniles to compete against larger fish for night feeding sites and daytime hiding cover, which we investigate in the following analysis. Another explanation is the greater importance of growth to the future fitness of juveniles: to reproduce, juveniles must grow as well as survive. For juvenile salmon in their first summer, growth is a higher fitness priority for individuals preparing to migrate to the ocean compared to individuals preparing to spend an additional winter in fresh water. Survival in the ocean is strongly dependent on size, so individuals migrating sooner need to grow faster. Metcalfe et al. (1998) found that salmon about to migrate spent more time foraging during the daytime than did salmon preparing to spend another winter in fresh water. Gries and Juanes (1998) observed more daytime feeding in age 1 than in age 0 Atlantic salmon and suggested that age 1 salmon, which are about to migrate to the ocean, are more motivated to grow. Valdimarsson and Metcalfe (1999) contrasted diel activity among salmon that did vs. did not outmigrate at one year and found daytime feeding much more prevalent among the salmon preparing to migrate instead of overwinter.

In our trout IBM, the effect of life history stage on selection of activity and habitat is represented by assuming that the fitness benefit of growth decreases as the size of reproductive maturity is reached: juvenile v-fish have a strong motivation to grow but this motivation decreases as adult size is reached. To directly test the effect of life history stage on diel activity patterns, we contrasted our baseline scenario to one in which life stage no longer affects the motivation to grow. This “no life history effect” (NLHE) scenario assumes that juveniles and adults all expect the same fitness benefit from growth. The NLHE scenario was implemented by replacing the logistic size function (Eq. 1) with a linear size function ($0.01 \times \text{expected length} + 0.4$). This linear function is simply a straight-line approximation of the logistic size function.

The test pattern that life history affects activity is reproduced if the NLHE scenario produces less difference (compared to the baseline scenario) between sub-adult (age 1) and older v-fish (age 3+) in the percentage of feeding that occurs in daytime. The NLHE scenario did in fact produce significantly less difference between age 1 and 3+ in daytime feeding ($P < 0.0001$). In the baseline scenario, 100% of age 1 feeding and 12% of age 3+ feeding took place in daytime, for a difference of 88%. In the NLHE scenario, 68% of age 1 feeding and 25% of age 3+ feeding took place in daytime, for a difference of 42%. (This remaining 42% difference indicates that factors other than life history stage also

influence diel activity patterns.) The IBM and SPHAST reproduced the observation that daytime feeding is more common among individuals that are in life stages with higher fitness motivation to grow.

Pattern 6: Competition increases diurnal feeding

Competition can cause salmonids to shift both the habitat and diel period used for feeding. In a laboratory experiment representing winter conditions, Harwood et al. (2001) found that competition caused Atlantic salmon to shift both the timing and location of feeding activity. When placed in competition with brown trout, some salmon shifted their nocturnal feeding to slower habitat and some became more diurnal. Alanärä et al. (2001) found similar results among brown trout: smaller trout avoided competition by feeding during day instead of night.

This test pattern is that competition from larger, night-feeding fish increases the fraction of feeding by smaller fish that occurs in daytime. We contrasted activity in age 2 v-fish under the baseline scenario (in which they compete with age 3+ v-fish) with activity in a “no age 3+” scenario that omitted the age 3+ class. In the baseline scenario, age 3+ v-fish feed primarily at night (Table 2) and younger v-fish feed during daytime. If the test pattern is reproduced, age 2 feeding becomes more nocturnal in the “no age 3+” scenario.

The expected effect of competition was reproduced in the IBM. When competition by age 3+ v-fish was eliminated, age 2 v-fish shifted from feeding primarily during day to feeding primarily at night. The mean percentage of age 2 feeding that occurred at night (over five replicates) changed from 5% in the baseline scenario to 60% ($P < 0.0001$).

Pattern 7: More daytime feeding when food availability or fish condition is low

Daytime feeding has been found to be more common in fish with low condition (low mass for their length), and when food availability is low or feeding conditions poor. Metcalfe et al. (1999) documented a trend of increasing daytime activity with decreasing food availability. Bradford and Higgins (2001) found higher daytime feeding in a stream reach with lower flows that likely provide poorer feeding conditions. Metcalfe et al. (1998) found a negative correlation between fish condition and level of daytime feeding. Metcalfe and Steele (2001) found daytime feeding to increase when condition was lower (food deprivation was longer) in minnows. A likely explanation for this pattern is that low condition or low food availability increase the risk of starvation enough that daytime feeding offers higher fitness despite its higher predation risk.

We based our simulation experiment on the laboratory experiment of Metcalfe et al. (1999), focusing on the influence of food availability on the relative frequency of nocturnal feeding. Metcalfe et al. observed what we use as a test pattern: the percentage of all

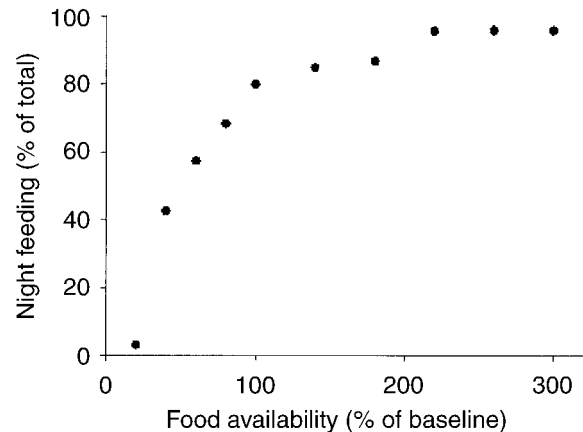


FIG. 3. Percentage of total feeding that occurs at night (number of v-fish feeding at night, divided by the number of v-fish feeding in daytime plus the number feeding that night) in v-fish 3+ years old, in relation to food availability. Each point represents one simulation.

feeding that occurred at night increased as food availability increased. We repeated our baseline scenario using a total of 10 food availability levels, ranging from 20% to 300% of the baseline food availability (using one model run per scenario). To avoid the confounding effects of competition, we examined only age 3+ v-fish.

The expected positive relation between percentage of feeding that occurs at night and food availability was reproduced by SPHAST (Fig. 3). As food availability increased, adult v-fish gradually shifted feeding from daytime to night feeding.

Pattern 8: Diel patterns vary with habitat

Physical habitat by itself can affect diel activity patterns. Bradford and Higgins (2001) observed major differences in diel activity at two sites on the same river, one site having flows greatly reduced by a diversion dam. In the trout IBM and in real streams, greatly reduced flows can provide less food, provide fewer sites with good velocities for feeding, and increase mortality risks because fish are easier for predators to see at lower depths and velocities. Another habitat factor investigated by Bradford and Higgins (2001) is availability of cover. If a fish does not have access to cover, hiding has little benefit and feeding may become the most beneficial activity.

The test pattern for this hypothesis is a general one: that changes in habitat can cause significant (and not always predictable) changes in activity. We simulated two additional scenarios. The “low-flow” scenario is identical to the baseline except that river flow was held constant at 15 m³/s instead of 60 m³/s. This reduction in flow reduces the area and diversity of habitat and, probably, the availability of good feeding sites. Therefore, the low-flow scenario is expected to increase the amount of time spent feeding, but it is not clear whether

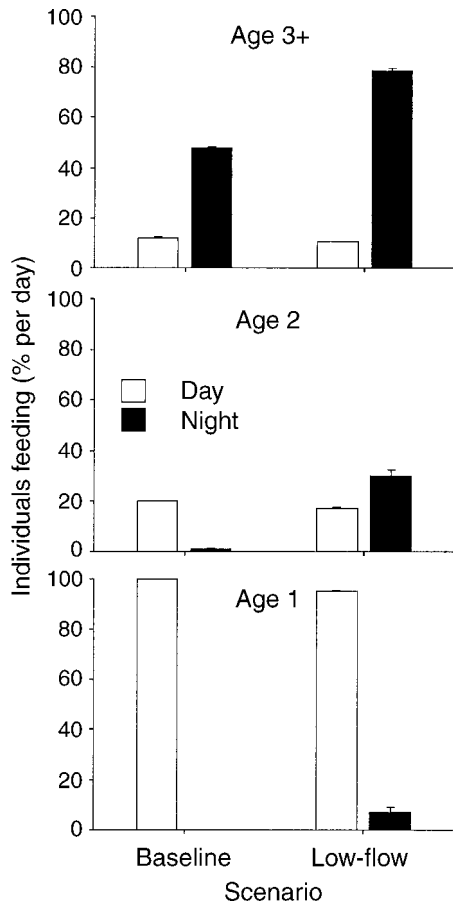


FIG. 4. Percentage of all v-fish that feed during day and night, in the baseline and low-flow scenarios at age 3+, age 2, and age 1 year. Results are means of five replicate simulations ± 1 SE.

the increase should be expected during day or night. The “low hiding value” scenario differs from the baseline in having reduced value of hiding cover: using hiding cover reduces predation risk by only 50% instead of by 99% in the baseline scenario. This scenario resembles the effects of sediment deposition, which can reduce the size and value of hiding cover. While we found no literature documenting diel behavior responses to reduced hiding cover, there is some experimental evidence (e.g., Armstrong and Griffiths 2001) that increased competition for hiding cover can increase the time salmonids spend feeding.

Altering habitat by reducing flow changed the v-fish activity patterns (Fig. 4). The reduction in flow generally had little effect on the percentage of v-fish feeding in daytime but greatly increased the percentage of v-fish that fed at night. For age 2 and 3+ v-fish, the differences between baseline and low-flow scenarios in the percentage of individuals feeding during night are significant at $P < 0.001$; for the percentage of individuals feeding during day, differences are significant at $P < 0.02$. T tests could not be conducted for age 1

because all baseline replicates produced 100% feeding during day. (The low-flow scenario did not produce lower v-fish survival, but did reduce growth.) The low hiding value scenario increased the total time spent feeding for all ages, with switches between daytime and night feeding varying among age classes (Fig. 5). Age 3+ v-fish remained primarily nocturnal but the relative frequency of diurnal feeding increased. Age 1 and 2 v-fish switched from feeding almost exclusively in the day to being primarily nocturnal, perhaps at least partly as a result of increased daytime competition from age 3+ v-fish. For ages 2 and 3+, differences between baseline and low hiding value scenarios in percentage of individuals feeding during day or night were statistically significant ($P < 0.0001$). Age 1 t tests could again not be conducted because there was no variation among baseline replicates.

CONCLUSIONS

SPHAST is a conceptually simple theory for how individuals make the joint decisions of what habitat to occupy and what activity (feeding or hiding) to pursue.

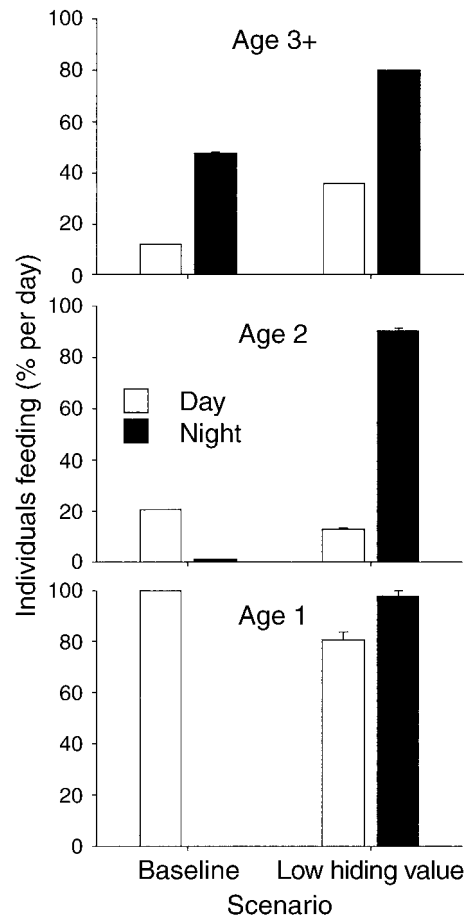


FIG. 5. Percentage of all v-fish that feed during day and night, in the baseline and low hiding value scenarios. The format is the same as for Fig. 4.

SPHAST assumes individuals select the combination of habitat and activity that maximizes expected future fitness, considering both day and night activity and the effects of both growth and survival on expected fitness. The theory, as implemented in the trout IBM, reproduced the eight test patterns of activity and habitat selection observed in field and laboratory studies of real salmonids. These results allow us to draw conclusions both specific to salmonids and general to the theoretical problem of understanding diel behavior patterns.

Concerning salmonids, our results confirm the belief of previous researchers (e.g., Fraser et al. 1995, Young et al. 1997, Heggenes et al. 1999, Bremset 2000, Alan-*ärä* et al. 2001, Bradford and Higgins 2001) that observed patterns of activity and habitat selection in salmonid populations emerge from multiple processes, including (1) variation among individuals in size, condition, and life history stage; (2) variation in feeding success and mortality risks with light level; (3) variation in metabolic rates with temperature; (4) the ways that habitat conditions affect food availability, feeding success, and hiding cover; and (5) competition among individuals for food and habitat. The numerous field and laboratory studies addressing this issue each provide strong evidence that one or several of these processes affect behavior. Our model shows that the effects of all these processes can be captured in a single, fitness-based framework for individual decision-making.

Patterns in diel activity are often assumed to have evolved genetically (e.g., Gries et al. 1997), but our results indicate that differences in diel activity pattern among sites, individuals, and even species can be explained without assuming animals have inherent tendencies to be nocturnal or diurnal. Observing that most feeding is nocturnal in one population and diurnal in another does not necessarily mean that the two populations have evolved different foraging traits. Instead, the different activity patterns may emerge from individual decision-making under different habitat or competitive conditions. Likewise, observing that some individuals feed during day and others at night at the same site does not mean that some individuals are inherently diurnal or nocturnal. Instead, the differences may emerge from individual variation in size, condition, and life history status.

The primary conclusion of broad theoretical interest from this study (and the previous study of Railsback and Harvey 2002, which focused on habitat selection) is that SPHAST appears to be a useful, general theory for how animals select diel activity and habitat under a wide variety of conditions. This theory is a way to combine information on how an individual's growth and mortality risks vary with diel phase, habitat, individual state, and activity into a single measure representing expected future fitness. The theory can be applied to a wide variety of problems by supplying it with appropriate growth and risk relationships. One

example is explaining the observation by Gregory and Griffith (1996) that hiding by fish is less common when turbidity (which reduces both feeding efficiency and mortality risk) is high. While our study focused on the highly variable diel behaviors of salmonids, the SPHAST approach should also apply to species with relatively constant diel patterns, such as some freshwater tropical (Arrington and Winemiller 2003) and marine (Reebs 2002) fish assemblages. While the specializations (e.g., shifting from deep water during day to shallow water at night, consistently nocturnal foraging) of some species appear clearly explained by physiological adaptations such as exaggerated sensing organs, specializations of other species are not yet clearly explained (Arrington and Winemiller 2003).

At an even more general level, this study confirms the state-based, predictive approach to modeling individual decisions as a useful toolbox that can be adapted to a variety of specific problems. The approach was originally developed to model habitat selection (Railsback et al. 1999) and was here expanded to include activity selection. The approach is conceptually similar to, and applicable to the same kinds of problems as, the dynamic state variable modeling theory (Houston and McNamara 1999, Clark and Mangel 2000). The primary difference between these two kinds of theory is that the state-based, predictive approach assumes individuals use a simple prediction of future conditions instead of a priori knowledge when estimating expected fitness over a time horizon.

It is important to remember that this study addresses population-level ecology, not behavioral ecology. Individual-based theory such as SPHAST is not intended to be a realistic, detailed model of an individual's behavior; instead, it is intended to be a simple model of what individuals do that is useful for explaining complex population behaviors and, ultimately, population dynamics (Railsback 2001, Grimm and Railsback 2005). SPHAST, as implemented in our IBM, may in fact be a very coarse model of what an individual animal does, but we have shown that the theory allows the IBM to reproduce a wide variety of population-level responses.

Finally, this study illustrates the value of pattern-oriented analysis of IBMs for developing theoretical understanding of complex ecosystem dynamics. (Other examples include Huse and Giske 1998, Railsback and Harvey 2002, and Stephens et al. 2002.) This approach is useful for finding relatively simple theory for how individuals interact with each other and their environment that can, when implemented in an IBM, explain realistic, complex, population dynamics. The habitat and activity selection problem we addressed is an example of dynamics that cannot be explained comprehensively by examining only the population or only the individuals; we must look at individuals in a population setting.

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