Table 3. Statistical analysis (χ^2) of results obtained on 10-min registering of test-fish positions

Groups tested	Class frequencies Positive	Neutral	Negative	χ^2	p
32 known → 32 unkw.	9	0	3	3	$0.1 < p < 0.05$
16 known → 16 unkw.	8	0	4	1.33	NS
8 known → 8 unkw.	7	0	6	0	NS
4 known → 4 unkw.	6	0	5	1.33	NS

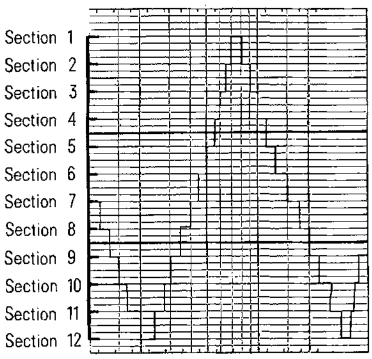

Figure 1. Example of test-fish position recording during 80 s. Abscissa: time-scale (1 mm = 1 s). Ordinate: sections of experimental trough relative to observer (section 1: extreme right; section 12: extreme left). The thick horizontal bars correspond to the position of sliding doors. In this example, the test-fish has moved from section 7 (middle of trough) to section 12 (extreme left) and from there to section 1 (extreme right).

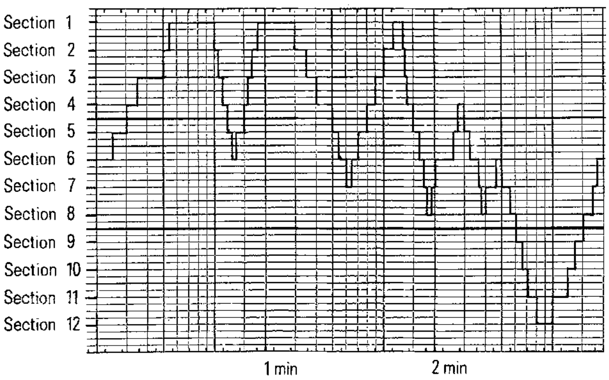

Figure 2. Example of graph (test fish No. 2 from group 8A) showing the 3 first minutes of recording. Ordinate: sections of experimental trough relative to observer (section 1: extreme right, where a water sample of group 8B was introduced; section 12: extreme left, where a water sample from group 8A, known to the test-fish, was introduced). Abscissa: time-scale (1 mm = 1.5 s). The thick horizontal bars correspond to the position of sliding doors. In this example, the test-fish moved mostly during the first 2 min, from section 6 to section 1 (which contained water from the known group); during the last min, the movements spread to all sections and became random.

a long parallelepiped (180 × 20 × 8 cm) divided into three 60-cm sections by sliding doors. The three sections were marked every 15 cm by black bars in order to facilitate localization. An electronic recorder made it possible to follow the test-fish continuously in its displacement along the 12 zones (180 : 15 cm) of the trough. The graphs thus obtained (figs 1 and 2) express the relative positions of the fish in the various zones and the corresponding time intervals it spent in each.

The experiments were performed in a room dimly and homogeneously illuminated by 36 W tubes, the water temperature being kept at 25.5 °C in accordance with natural conditions[5]. The fishes were not fed during the 24 h prior to the experiment. The experiments were conducted as follows: the test-fish was placed in the central section of the aquarium, where it remained for 2 min with all the sliding doors shut. During this time interval, two water samples (500 ml each) drawn from home aquariums were delivered at either end of the trough with the help of baxter bottles, using a table of random numbers in such a fashion that each individual bottle was placed an equal number of times at either end. The doors were then lifted and the displacements of the fish were registered during 10 min. Four series of 12 experiments were carried out under these conditions.

The overall results show that juvenile cavernicolous *A. mexicanus* discriminate significantly between two samples of water containing chemical traces from known or unknown conspecifics, kept in separate home-tanks at equal densities (table 1). They display a significant locomotory response ($p < 0.01$) towards the traces of the known group during the first 2 min of the experiment (table 2). After this time-interval, exploration becomes random (table 3). A similar phenomenon was previously noted by Berti et al.[3] with adult *Phreatichthys andruzzii*, which swim directly in the direction of traces of known conspecifics, but only after 9 min towards those of unknown ones, in both cases compared with a neutral stimulus (distilled water). It appears therefore that *A. mexicanus* recognizes the odor of conspecifics, and shows moreover a tendency to orient itself preferentially towards known ones during a short time, but the fairly quick fading of the response in these conditions of choice has still to be explained. An accurate determination of the chemical traces actually at work is needed to devise further experiments able to throw light on the specific factors determining the preferential response observed.

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Risk-sensitive foraging by a migratory bird *(Dendroica coronata)*[1]

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Summary. Because migration is a period of exceptional energy demand, individuals in migratory disposition should be particularly sensitive to variability in food availability, i.e. show risk-sensitivity in their foraging behavior. When given the opportunity to feed at either a constant or a variable reward station, birds in migratory disposition (experimentals) chose the variable reward (risk-acceptance) more often than the constant reward during the premigratory fattening period as they gained weight and accumulated an energy reserve, while control birds not in migratory disposition consistently preferred the constant reward (risk-aversion). Once birds in migratory disposition attained maximum body weight and began to show nocturnal restlessness, their behavior changed and they, too, behaved in a risk-averse manner.

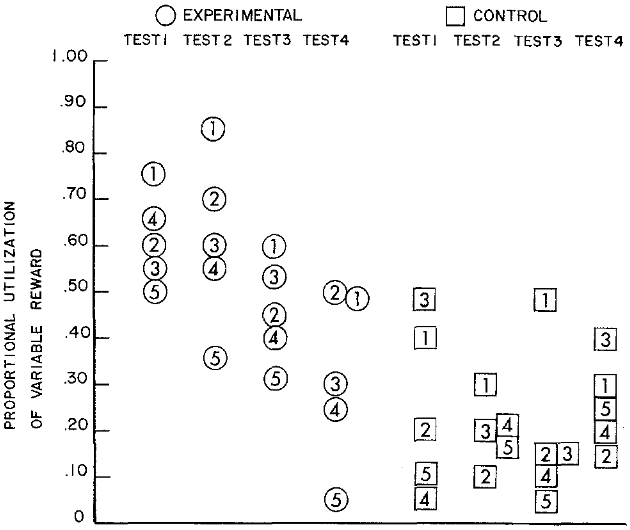
Key words. Bird migration; foraging behavior; risk-sensitivity.

The seasonal migrations that characterize much of the world's avifauna are energy-expensive, high risk events[2,3]. Migratory flights are longer in duration and energetically more costly than flights undertaken during non-migratory periods; levels of metabolic effort during migration are estimated to be 5–10 times the standard metabolic rate[4]. Migratory birds must contend with fluctuations in food availability, heightened risk from predators, competition among themselves and with residents at stopover sites, the vicissitudes of weather, and possible orientational errors[5-11]. How well migrants respond to the contingencies associated with migration surely has an impact upon their survival and future reproductive success. Consequently, migratory populations are likely to have evolved behavioral responses that reduce the risks associated with migration or enable individuals to efficiently meet energy demands. For example, we[12] recently found yellow-rumped warblers *(Dendroica coronata)* to be especially efficient foragers while in migratory disposition. Experimental birds adjusted their feeding behavior to 1) consume more food items per feeding bout, 2) handle items more rapidly, thereby increasing the net energetic value of the food they consumed, and 3) select more profitable food items relative to control individuals that were not in migratory disposition. Warblers are more likely to chose food items on the basis of energetic costs and benefits when feeding considerations are likely to have considerable impact on survival and future reproductive success[13,14]. Foraging models that predict animals should maximize their mean rate of energy gain make the simplifying assumption that foragers are indifferent to variability in food reward. Yet foraging preferences should reflect not only the various mean rewards, but also the variances in foraging benefits[15-17]. When there is uncertainty attached to the outcome of foraging behavior, individuals should be sensitive to variance in reward and might try to minimize the uncertainty associated with outcomes (i.e., foragers will generally avoid risks and prefer to exploit a constant food resource thereby diminishing the possibility of doing poorly). If the forager prefers to exploit a variable resource, its behavior is said to be risk-prone. When a forager anticipates an energy deficit, its utilization of more variable resources is likely to increase. Risk-prone behavior is adopted because it maximizes the probability of obtaining enough food to meet daily energy demands. Migration is a period when foragers experience high energy demands and the possibility of a net energy deficit. Daily energy demands are great for migrants during the premigratory fattening period as they accumulate energy stores as well as during the en route period when energy stores are depleted during migratory flights and must be replenished[18,19]. We hypothesized that yellow-rumped warblers in migratory disposition should be risk-sensitive and more likely to forage in a risk-prone manner relative to control individuals not in migratory disposition. Migratory disposition refers to the specific physiological state leading to a general metabolic condition in which there is sufficient energy available for migration[2].

Materials and methods. Yellow-rumped warblers are North American migrants whose breeding range extends from Alaska and northern Canada through the coniferous forest into the northern United States. They winter abundantly throughout the southern half of the United States east of the Great Plains and south to Panama. The warblers were mistnetted in November 1984 in southcentral Mississippi near Hattiesburg, Mississippi, USA. In the first part of January birds were moved to individual activity cages and assigned randomly to control ($n = 5$) and experimental ($n = 5$) groups. Prior to experimentation, birds were housed in group flight cages under winter (LD 10:14) photoperiod while being fed a diet of commercial monkey biscuits, larvae of *Tenebrio molitor*, and supplemental vitamins and minerals. Migratory disposition (characterized by body weight increase, subcutaneous fat deposition, and nocturnal restlessness was induced in the experimental birds at this time by exposing them to long (L D 16:8) daylengths. Daylength was increased by 1 h daily increments until a 16-h day was reached (LD 16:8). During the premigratory fattening period, before the onset of migratory restlessness, experimentals gained, on average, 3.9 g which represented a 31% increase over their pretest weight. Between 20 and 25 days following the photoperiod change, the caged migrants began to display nocturnal restlessness. Control birds that remained on a short day (LD 10:14) photoperiod maintained constant weight throughout the experiment and did not display nocturnal restlessness. The ability to induce a migratory state in experimental birds enabled us to conduct simultaneous feeding tests with controls and experimentals.

The design of our risk-sensitivity experiment was essentially the same as that developed by Caraco and his associates[15,16]. During an experiment, birds were deprived of their normal diet for 2 h and tested in a cage (60 × 60 × 60 cm) equipped with two feeding stations access to which was remotely controlled by the experimenter. A constant reward of 3 small larvae (8–12 mm long) of *Tenebrio molitor* was presented at one station with a probability of 1, whereas a variable reward was presented at the other station. The variable reward provided either 0 or 6 larvae, each with a probability of 0.5. The expected value of the variable reward always equalled the constant reward. Because the means are equal and the variable reward was symmetric about its expectation, a preference for one station should indicate a response to benefit variance.

In order to learn the differing reward characteristics prior to the experiments, each bird underwent a series of 15 forced-choice trials during which only one station provided food. Twenty preference trials immediately followed the learning trials. The two feeding stations were exposed simultaneously and the birds selection recorded. Once a station was selected, access to the other station was precluded. Two sets of learning trials plus preference trials were conducted 2 days apart during the premigratory fattening period, while experimentals gained weight and deposited subcutaneous fat. These experiments were followed by two additional sets of learning trials plus preference trials after experimentals attained maximum body weight and were displaying nocturnal restlessness (designated the migratory period). After an experiment with each bird, we tested for position ef-



Proportional utilization of the uncertain (variable) reward over all trials for experimental (circles) and control (squares) birds during the premigratory period (tests 1 and 2) and migratory period (tests 3 and 4). The responses of the 5 experimental and 5 control birds are numbered according to individual. The variable reward is preferred significantly ($p < 0.05$) when the proportional utilization is ≥ 0.70. The constant reward is preferred significantly when the utilization is ≤ 0.30. Otherwise the birds were indifferent with respect to the two reward situations.

fects[15]. When not involved in an experiment, warblers had ad libitum access to food.

Results. We first tested the null hypothesis of no difference between the control and experimental birds. With the exception of E5, the 5 birds in migratory disposition (experimentals) selected the variable station more often than the constant station during the premigratory fattening period (fig.). Control birds, on the other hand, clearly preferred the constant reward during the same period. Contingency table analysis of the group totals for both pre-migratory tests confirms the rather obvious difference: $\chi^2 = 25.45$ ($p < 0.001$) and $\chi^2 = 30.53$ ($p < 0.001$). After experimental birds attained maximum weight and deposited subcutaneous fat (migratory period: tests 3 and 4), they switched their preference and opted more often for the constant reward (fig.). Their behavior was statistically indistinguishable from controls by the time they were tested the second time (test 4) during this period ($\chi^2 = 1.15$, $0.25 < p < 0.50$). The change in preference among the experimentals from test 2 of the premigratory period to the test 3 of the socalled migratory period was statistically significant ($p < 0.05$) according to a McNemar's test[20] for significant change ($G_{adj} \approx \chi^2_{0.05(1)} = 4.17$). Note further that experimental birds, with the exception of E2, became more risk-averse between test 3 and 4 of the Migratory Period.

If the behavior of individual birds is tested against the null hypothesis of indifference (equal preference), the hypothesis is rejected ($p < 0.05$) by the cumulative binomical probability function when one station is selected 14 or more times. These results, too, indicate that yellow-rumped warblers are sensitive to variation in energetic rewards. During the premigratory fattening period, experimental birds behaved in a risk-prone manner or behaved indifferently (fig.), with the exception of E5 who preferred the constant reward during test 2. Control birds were essentially risk-averse at this time. Controls continued to avoid the variable reward when retested after experimentals attained maximum weight and began to show migratory restlessness. At the same time, experimental birds changed their behavior and now behaved indifferently or were risk-averse (fig.).

Discussion. Two important conclusions emerge from the results of our experiment. First, yellow-rumped warblers are not indifferent to variance in food reward. Although this may not be an especially surprising result, only a few studies have demonstrated both risk-prone and risk-aversive behavior in the same species[15–17,21]. Moreover, yellow-rumped warblers are more likely to be risk-prone at a time when energy demands are higher and the possibility of a negative energy budget greater, i.e. while accumulating the fat reserves so critical to a successful migration. Second, individuals in migratory disposition change from risk-acceptance to risk-aversion with respect to their foraging behavior after they deposit fat reserves, attain maximum weight and begin to display nocturnal restlessness. This response corresponds to a fitness characterization (*sensu* L. Real[21]) that is sigmoidal with a convex segment followed by a concave segment; the individuals in migratory disposition first prefer risk then prefer certainty.

Results of food deprivation studies point to a relationship between risk sensitivity and daily energy budgets: Be risk prone when your daily energy budget is below that required for survival. Our results clearly demonstrate that experimental birds switch at a biologically meaningful point but at no time are they experiencing a negative energy balance. During the premigratory fattening period while experimental birds were hyperphagic and accumulating fat deposits, the expectation of meeting projected energy demands might have been lower given the experimental conditions, hence their risk-prone behavior relative to controls not in migratory disposition. Once lipid was accumulated and the individual entered the so-called migratory period, experimental birds could presumably maintain the new level of lipid (energy stores) without increasing intake as long as total energy expenditure did not increase[12,22]. At this time, they became risk-averse like control birds. Our results lend support to the general notion of a target level with respect to an individual's energy balance but question the original interpretation of the z-score model and other survivorship models[23].

Obviously, the energy expenditure from a night of nocturnal locomotor activity in a laboratory cage is considerably less than that associated with a night's migratory flight. We would expect that risk-sensitive foraging would be advantageous in the field when energy reserves are depleted following a night's migration and migrants are under strong selective pressure to replenish reserves rapidly at stopover sites. One of the most, if not the most, important purposes for which stopover habitat is used by migrating birds is as a place where energy reserves can be replenished before continuing migration. Although most, if not all migrations are likely to be in migratory disposition while en route, their energy reserves and hence their energy demand will vary depending upon en route circumstances[9,19,24,25].

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