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Report

The Survival Advantage of Olfaction in a Competitive Environment

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Summary

Olfaction is generally assumed to be critical for survival because this sense allows animals to detect food and pheromonal cues. Although the ability to sense sex pheromones [1–3] is likely to be important for insects, the contribution of general odor detection to survival is unknown. We investigated the extent to which the olfactory system confers a survival advantage on *Drosophila* larvae foraging for food under conditions of limited resources and competition from other larvae.

Results and Discussion

This study utilized anosmic *Or83b* mutant larvae, which lack the essential olfactory coreceptor Or83b [4, 5]. Although *Or83b* mutant larvae lack behavioral responses to odors [4, 5], they show normal viability under standard laboratory rearing conditions that feature abundant food resources. We reasoned that a survival advantage of the olfactory system might be revealed in seminatural conditions in which *Or83b* mutant larvae are challenged to forage for limited food resources.

We developed a survival assay in which either 10 or 50 embryos were introduced into 100 mg of fly food in the center of a 150 mm circular arena at 1 day after egg laying (AEL). At 3 days AEL, a second 100 mg food source supplemented with 70 mg live-yeast paste was introduced 70 mm away from the first food source (see Figure S1A and Supplemental Experimental Procedures, available online). Larvae hatch on the first food source, and if this is exhausted by 3 days AEL, they must locate the second food source to continue eating. Because the assay is carried out in the dark, we presume that larvae primarily use chemosensory cues to find the second food source. The number of newly emerged adult flies was counted daily from 10 to 20 days AEL, and these data were used to generate cumulative eclosion-rate plots, a direct measure of embryo-to-adult survival.

We compared the survival of anosmic *Or83b* mutants to control animals in which *Or83b* was genetically rescued in all olfactory neurons ("*Or83b* functional"). Normal olfactory behavior is known to be restored in *Or83b* functional animals [4, 5], and their rate of survival did not differ from that of wild-type strains in our assays (data not shown). Both anosmic *Or83b* mutant animals and control *Or83b* functional animals showed indistinguishable high adult survival rates at low population density regardless of whether a second food source was supplied (Figure 1A). This result demonstrates that *Or83b* mutants do not have a nonspecific survival deficit independent of the known olfactory phenotype. When food was limited and larval density was high, both *Or83b* mutant animals and *Or83b* functional animals showed severely reduced survival (Figure 1B, left). When a second food source was provided at a distance, *Or83b* functional animals showed a significantly higher survival rate than that of *Or83b* mutants (Figure 1B, right). To test whether restoring partial olfactory function sufficed for survival when a second food source was supplied, we rescued *Or83b* function in only the pair of olfactory neurons expressing *Or42a* ("*Or42a* functional") [5]. *Or42a* functional larvae showed a survival rate indistinguishable from that of *Or83b* functional animals in all conditions tested (Figures 1A and 1B), a finding that we attribute to the broad tuning of the generalist *Or42a* receptor, which is sensitive to fly food [6] and a large number of fruit odors [7].

Whereas *Or83b* functional control larvae left the first food, located the second food, and pupated, most *Or83b* mutant larvae failed to exploit this secondary resource (Figures 1C and 1D). This confirms that olfactory impairment directly impacts the survival ability of *Or83b* mutants. *Or42a* functional larvae showed intermediate migration to the second food source, suggesting that larvae with a partially functioning olfactory system are slightly less efficient than *Or83b* functional controls in finding the second food source. The survival of *Or83b* mutants was not affected by switching the location of the first and second food sources (Figure S2A) or by omitting propionic acid, a taste chemical that *Or83b* mutants can perceive [4], from the fly food (Figure S2B).

The poor eclosion rate of *Or83b* mutants in conditions of high density and limited food suggests that the lack of a functioning olfactory system could prove to be a disadvantage when larvae are challenged to compete. We designed a competition assay that was carried out in exactly the same manner as the survival assay except that equal numbers of embryos from both wild-type and *Or83b* mutant strains were introduced together onto 100 mg of food and supplied with a second food source at 3 days AEL (Figure S1B). Newly eclosed adults of both strains were genotyped and counted in the same manner as in the survival assay.

When five *Or83b* functional control embryos and five *Or83b* mutant embryos were introduced, both strains showed indistinguishable cumulative survival rates, but *Or83b* mutants eclosed more slowly (Figure 2A, left). When 25 or 40 embryos of each strain were introduced, both the eclosion rate and total number of eclosed adults of *Or83b* mutants were significantly different from those of *Or83b* functional animals (Figure 2A, center and right), Thus, anosmic *Or83b* mutants were selectively eliminated in competition with control animals at high density.

To investigate whether a single pair of olfactory sensory neurons (OSNs) could restore larval competitiveness, we competed *Or42a* functional animals against *Or83b* mutants. When 25 or 40 embryos of each strain were introduced, the survival of *Or83b* mutant animals was severely reduced in the presence of *Or42a* functional animals (Figure 2B). Finally, we observed

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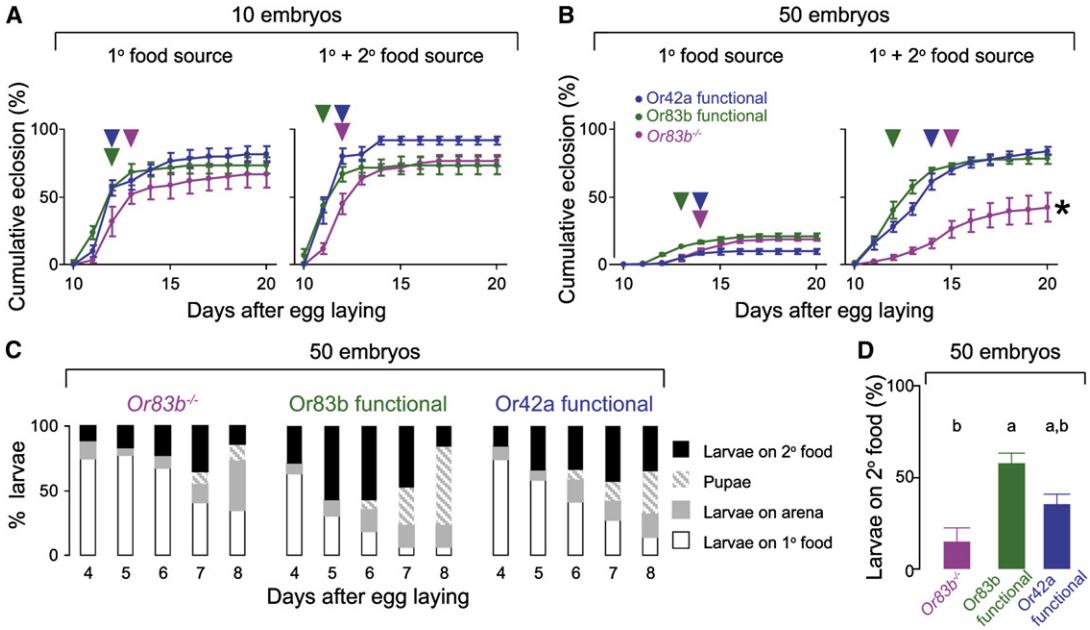

Figure 1. Anosmic *Or83b* Mutant Larvae Show Reduced Survival and Fail to Exploit a Secondary Food Source

(A and B) Cumulative eclosion rates of *Or83b* functional (green), *Or83b* mutant (magenta), and *Or42a* functional (blue) flies from either 10 (A) or 50 (B) embryos in the absence (left) or presence (right) of a second food source are plotted against days AEL (mean ± SEM, n = 6). Half-maximal eclosion rates are indicated with an arrowhead. The cumulative eclosion rate did not differ across genotypes with ten embryos (A), but the cumulative eclosion rate of *Or83b* mutants was significantly lower than that of the three other genotypes when the second food source was supplied to 50 embryos (B) (ANOVA and post hoc Tukey's HSD test; the asterisk indicates a 99% confidence level).

(C) Distributions of *Or83b* mutant (n = 7), *Or83b* functional (n = 4), and *Or42a* functional (n = 5) animals from 4 to 8 days AEL are shown in stacked bar plots.

(D) Percentage of larvae accumulating on the second food source at 5 days AEL (mean ± SEM). Bars that are statistically different are labeled with different letters (ANOVA and post hoc Tukey's HSD test; 99% confidence level).

that *Or42a* functional animals showed delayed eclosion and reduced survival when competing against control *Or83*b functional animals at high population densities. Therefore, although larvae with one pair of functional *Or42a*-expressing OSNs are competitive against anosmic *Or83b* mutant animals, they perform less well when compared to larvae with 21 functional OSNs. Fly food is likely to emit a complex mixture of volatile chemicals, many of which would not be detected by the

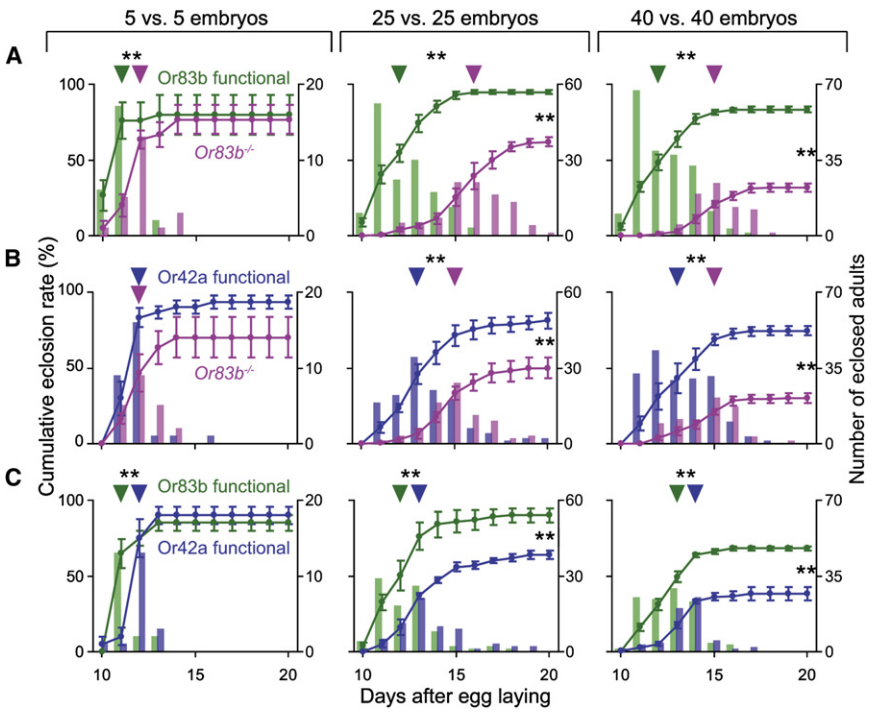

Figure 2. Survival of Anosmic *Or83b* Mutants Is Further Reduced by Competition with Larvae that Detect Odors

(A–C) Cumulative eclosion rates (mean ± SEM) from competition of *Or83b* functional versus *Or83b* mutant larvae (n = 6) (A), *Or42a* functional versus *Or83b* null mutant larvae (n = 6) (B), and *Or42a* functional versus *Or83b* functional larvae (n = 4) (C) for 10 (left), 50 (middle), and 80 (right) total embryos. Values of cumulative eclosion (y axis at left) that differ statistically between genotypes are indicated with black asterisks placed at the right of the eclosion curves (Student's t test; $^{**}p < 0.01$). Overlaid bar plots (y axis at right) indicate the total number of adults eclosing on each day from 10 to 20 days AEL. Half-maximal eclosion rates for each genotype are indicated with an arrowhead, and eclosion distributions that differ statistically between competing strains are indicated with black asterisks placed above the arrowheads (Kolmogorov-Smirnov; $^{**}p < 0.01$). Unmarked comparisons are not significant by the same tests ($p > 0.05$).

Or42a OSN. This suggests that a fully functional olfactory system confers additional advantages in exploiting a distant food source for survival.

Conclusions

Our results provide the first direct evidence that the sense of smell is necessary for effective foraging and survival to adulthood in *Drosophila*. Although these animals are deposited on food sources by their mothers, our results suggest that the larval sense of smell is indeed useful for finding food beyond the site of oviposition. In conditions of high population density and limited food, the loss of a functional olfactory system selectively impairs survival. We believe this is because resources at the site of oviposition are depleted under such conditions, making it necessary for animals to disperse to obtain food. Such competitive conditions may be faced by these animals in their natural environment [8, 9]. Although our experimental conditions are artificial, we speculate that many insects face resource scarcity in their natural environment, and therefore our findings are likely to be relevant beyond laboratory-reared fruit flies. We suggest that impairment of olfactory function will reduce insect competitiveness and thus may be useful in insect-control strategies that target the sense of smell.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two figures and can be found with this article online at http://www.current-biology.com/cgi/content/full/18/15/1153/DC1/.

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