

TRACKING DISSOLVED OXYGEN LEVEL THROUGH AN ORGANIC RAINBOW TROUT FARM AT CUERICÍ, COSTA RICA

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Abstract: Dissolved oxygen (DO) is essential to aquatic life and frequently limiting. We evaluated the relative importance of environmental factors on DO by measuring changes in DO through an organic rainbow trout aquaculture system at Cuerici, Costa Rica. We predicted that dissolved oxygen would decrease with increased temperature and respiration, and increase with photosynthetic activity, but we could not predict the relative importance of these forces. We found that photosynthetic index (a composite measure of algal abundance and sunlight), and not temperature or respiration, was the best predictor of DO level. Water temperature was quite stable throughout the aquaculture system at about 12°C, and was unrelated to dissolved oxygen. Surprisingly, the biomass of trout within pools, which reached as much as 6.4 kg of trout per m³, also had no detectable effect on dissolved oxygen levels.

Keywords: rainbow trout farm, dissolved oxygen, water temperature, photosynthesis, respiration

INTRODUCTION

Oxygen is one of the most important elements for life on earth. Due to its poor solubility in water, oxygen is an especially important limiting factor in aquatic ecosystems. As humans increase in number, it becomes increasingly important for us to understand how our activities influence biologically important environmental features such as dissolved oxygen (DO) in aquatic ecosystems.

We conducted a study of dissolved oxygen within the aquacultural system of an organic rainbow trout farm at Cuericí Biological Station, Costa Rica. Our objective was to assess the relative importance in this system of the

various physical and biological factors that are known to influence dissolved oxygen. We hypothesized that DO level would change throughout the trout farm due to changes in one or more of these factors including temperature, photosynthesis, respiration, water flow and surface area to volume ratio of trout pools.

These factors, and their interaction(s), can affect DO of streams and ponds in ways that are generally well understood. Algal photosynthesis tends to increase DO because O₂ is a chemical product of photosynthesis. Water temperature affects DO level because warmer water has the physical property of holding less oxygen at saturation than cooler water. Warmer water should also tend to decrease DO because

increasing temperature increases the respiration rate (i.e., O₂ use) of fish, microbes, and other organisms living in the water. Increases in trout biomass relative to the size of pools is expected to decrease DO because more trout biomass means more O₂ depletion (both from the trout directly and from the microbes that are decomposers of trout feces). Increased water flow and surface area to volume ratio increases DO by increasing atmospheric oxygen input via increased aeration and diffusion area.

METHODS

We collected water quality and temperature measurements at 22 sites (numbered from upstream to downstream) along the trout farm at Cuericí Biological Station, Costa Rica (Figure 1). We measured DO, pH, water temperature and air temperature at each site at 1830 on 31 Jan and at 1030 and 1430 on 1 Feb 2008. We also rated algal content on an ordinal scale of 1 to 5 (lowest to highest) scale and categorized sunlight exposure as 1, 2, or 3 (shade, partial sun, or sun, respectively). We multiplied these two values to calculate a photosynthetic index for each site. For each tank or pond, we also measured water surface area, water volume, and estimated fish biomass. We interpreted fish biomass as a proxy for oxygen depletion by respiration from fish and associated microbes.

To determine which factor(s) best predicted DO, we evaluated all possible linear regression models involving one or more of the six putative drivers of DO: site number (upstream to downstream), water temperature, photosynthetic index, flow: volume, surface: volume, and biomass: volume. Models were compared with respect to Akaike's Information Criteria (AIC).

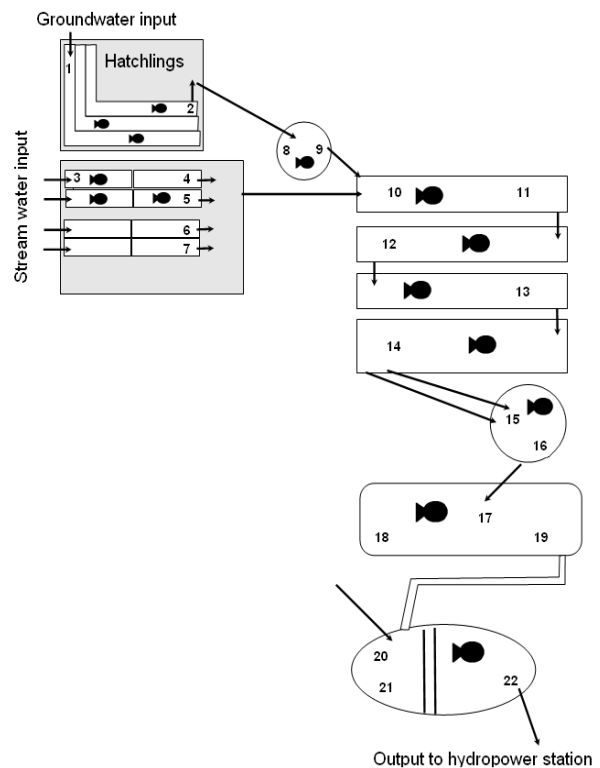


Figure 1. Map of rainbow trout farm at Cuericí Biological Station, Costa Rica. We chose 22 sampling sites at the input and output of each tank or pond, beginning upstream (1) and ending downstream (22) of the system.

RESULTS

The rainbow trout farm contains 12 fish pools of various sizes (volume: 3.5 - 478 m³, surface area: 8.8 - 395 m²). Trout are grouped by size, beginning with hatchlings upstream (up to 3 months age). Fish are moved downstream as they grow so fish size increases from upstream to downstream.

Average trout mass ranged from 1.26 g (hatchlings), to 433 g (adults), to 2167 g (breeders). Number of fish ranged from ca. 45,000 in the hatchery (sites 1-7), ca. 400 in troughs (sites 10-14), ca. 200 in breeder pools (sites 8-9, 15-16, 20-21), and ca. 25,000 in lakes (sites 17-19, 22). Two pools in the hatchery contained no fish (sites 6 and 7).

Mean flow rate ranged from 0.53 - 4.6 L/s with an average flow rate of 3.34 L/s. Water pH varied between sites ($F = 23.00$, $df = 22$, $P < 0.0001$), but did not significantly increase or decrease through the trout farm ($F = 2.10$, $df = 1$, 42 , $P = 0.016$, $r^2 = 0.05$) or in relation to fish abundance ($F = 1.81$, $df = 1$, 64 , $P = 0.18$, $r^2 = 0.03$). Because pH only ranged from 6.5 to 7.0 (mean \pm SD 6.8 ± 0.12), we doubt that this variation was biologically meaningful.

The average concentration of dissolved oxygen varied among sampling locations (range = 5.23 - 8.67 mg/liter; $F = 8.85$, $df = 21$, 42 , $P < 0.0001$) and sampling times (repeated measures ANOVA, $F = 46.84$, $df = 2$, 42 , $P < 0.0001$). Because there was no

interaction between site and time (based on visual assessment of the data since the data structure precluded a formal test), we averaged DO across time for the remainder of the analysis. Surprisingly, DO level was also higher at 1830 than at 1030 and 1430.

Contrary to our prediction, DO level did not decrease with increasing temperature ($F = 2.29$, $df = 1$, 20 , $P = 0.15$, $r^2 = 0.07$). The ratio of fish biomass: pool volume was also unrelated to DO ($F = 0.22$, $df = 1$, 20 , $P = 0.65$, $r^2 = 0.01$).

Of all possible linear models involving any combination of the six theoretical drivers of DO that we measured (site number, water temperature, photosynthetic index, flow:volume, surface:volume, and/or biomass:volume), a model that included photosynthetic index alone emerged as the best model (Table 1, $\Delta AIC > 10.3$ compared to any alternative model). Across the range of photosynthetic indices in our study system, average dissolved oxygen increased from 5.23 to 8.67 mg / liter (Figure 2. $F = 15.68$, $df = 1$, 20 , $P = 0.0008$, $r^2 = 0.44$). None of other independent variables were significantly related to DO in simple linear regressions. For example, fish biomass relative to tank or pool water volume (biomass: volume) was unrelated to DO ($r^2 = 0.01$, $df = 1$, 20 , $P = 0.65$).

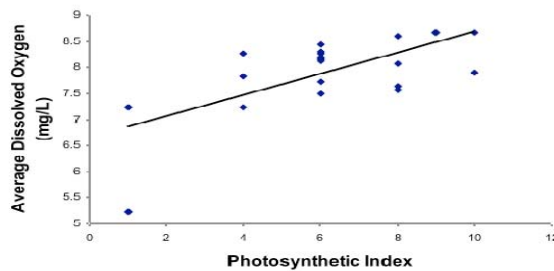


Figure 2. Relationship between photosynthetic index (1-low to 15-high) and average dissolved oxygen at Cuericí Biological Station, Costa Rica.

DISCUSSION

Photosynthetic index was the best predictor of DO. Apparently, of all variables tested, oxygen produced by photosynthesis had the largest effect on changes in DO levels. While photosynthetic index was the best statistical predictor of DO, other factors such as temperature, algal mass: volume, and water depth can also influence the rate of photosynthesis. So the full causal pathways could involve other variables.

If photosynthesis is an important driver, it is expected that there would be diurnal cycles in DO associated with diurnal cycles in photosynthetically active radiation. Indeed, the highest DO that we measured was at 18:30 on the first night, which might have reflected the accumulation of DO over the day from photosynthesis. However, the dissolved oxygen meter malfunctioned after the first reading, requiring that we change the

membrane and re-calibrate the meter. Thus the higher DO measurements at 18:30 could have been an artifact. Future studies that include repeated day and night measurements could easily resolve the question of whether the pattern we reported is indeed driven by photosynthesis, rather than other factors positively correlated with photosynthesis.

It seemed surprising that there was no effect of fish biomass on DO. Some pools had no fish, while one (site 17, 18, 19) contained about 25 1000-g trout in 478 m³ of water. Based on the general interspecies relationship, the expected respiration rate of a 1000 g poikilotherm at 12 °C is about 410 ml O₂ · kg⁻¹ · h⁻¹ (Peters 1983), which seems like it could have measurably depleted DO within the pool, especially in combination with decomposition of trout feces. However, it seems that this respiration is modest relative to the constant input of oxygen from the inflow of water, photosynthesis within the tank, and/or diffusion of O₂ from air into sub-saturated water. In any case, it seems that this aquaculture system is presently not DO limited.

As human impact on the environment increases, it becomes increasingly important to understand the factors that influence DO level in aquatic ecosystems. Our study shows that, among other factors, photosynthesis of aquatic vegetation

is important in determining DO level in aquatic systems.

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Table 1. Models of individual variables affecting dissolved oxygen level in a rainbow trout farm at Cuericí Biological Station, Costa Rica.

| Variables | Biological Reason | R² | AIC value |
|------------------------------------|---|----------------------|------------------|
| Photosynthetic Index (PI) | Increased photosynthesis increases D.O.. | 0.44 | -22.7 |
| Water Temperature (T) | Decreased water temperature increases D.O | 0.10 | -12.4 |
| Flow: Volume (F:V) | Increased water flow increases D.O. | 0.08 | -11.9 |
| Surface area: Volume (SA:V) | Greater SA:V allows more atmospheric oxygen to enter | 0.03 | -10.8 |
| Biomass: Volume (B:V) | Increased fish respiration and decomposition decreases D.O. | 0.01 | -10.3 |

GROUP FORAGING ACTIVITIES OF LARGE-FOOTED FINCHES

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Abstract: Foraging in species-specific groups should generally lead to reduced foraging success, as conspecifics compete for the same resources. However, many species consistently forage in groups. To help explain this paradox we observed the foraging and movement patterns of Large-footed Finch (*Pezopetes capitalis*) groups in Cerro de la Muerte, Costa Rica. We speculated that foraging in groups is an adaptation to aid foraging success by increasing the efficiency of prey discovery. This would require that resources be aggregated in space, which was supported by temporal aggregation of attacks. The optimal foraging model further predicted that attack rates by individual finches would increase with increasing group size and member proximity, and that groups would be relatively stable. As predicted, attack rate was higher ($>2\times$) in finches within 60 cm of another finch. However, attack rates were not higher in larger groups. This suggests foraging benefits for finches in pairs, but no additional benefits for larger groups. Studies of group composition and movement verified that pairs tended to forage together, and detected 6 of 20 groups that included more than 2 adults.

Keywords: bird behavior, time allocation, social groups, Cuericí, Costa Rica, Cerro de la Muerte, resource aggregation

INTRODUCTION

Foraging in the vicinity of conspecifics should commonly diminish foraging success because of resource competition. Some organisms however, routinely forage in groups. One potential explanation is that the costs of increased competition are compensated by reduced risks of predation due to group vigilance. Grouping may also allow vigilance duties to be shared, allowing individuals within groups more time to forage.

Predation risks aside, there are probably some circumstances under which individuals within groups might acquire prey more

efficiently than singletons. This is most likely if prey items are spatially aggregated and if there are emergent benefits from group foraging (e.g., if activities of one individual can flush prey items for a nearby individual).

We studied how grouping behavior affects the foraging of Large-footed Finches in Cerro de la Muerte, Costa Rica. These birds pair-bond throughout the year (Stiles and Skutch 1989), but are also reported to form larger groups. We evaluated three predictions derived from the hypothesis that group foraging by Large-footed Finches is an adaptation to enhance resource acquisition by individuals: (1) prey attack rates should increase with

increasing group size and member proximity; (2) the groups are expected to be reasonably stable while foraging and not just incidental fission-fusion encounters; and (3) prey attack rates will tend to be aggregated in time, indicating that prey are aggregated in space.

Of course, birds could forage in groups for reasons other than to increase foraging efficiency. For example, finches may forage in family groups, as parents tolerate competition from their offspring as a cost of reproduction. Also, pairs may remain together to ensure access to a mate throughout the year (Stiles and Skutch 1989). To evaluate these possibilities we tried to determine whether foraging groups commonly contained more than two adult birds, in which case they could not be family groups.

METHODS

On 1-2 February 2008, we observed 20 groups of *Pezopetes capitalis* near the Cuericí Biological Station in Cerro de la Muerte, Costa Rica. For each group, we recorded group size and recorded prey attack rates for as long as we could remain with the flock. To estimate prey attack rates, we followed a focal individual for as long as we could keep it in sight, continuously recording attacks as they happened. Attacks were defined as visible ground pecks. We recorded the

number of attacks in 10 second intervals and scored the bird as being near or far from the nearest other finch (with “near” defined as within 60 cm). The duration of sustained observations on focal individuals ranged from 10 seconds to 8 minutes. When we lost sight of a focal bird, we switched to a different bird in the same flock, starting a new observation bout. When we lost a flock, we searched for a different flock and restarted the procedure.

For analyses, we calculated for each focal individual ($n = 54$) the average of attacks / 10 sec for all observations where the bird was near to another finch and all observations where the bird was far from the nearest finch. We square-root transformed the data to improve normality, then performed a one-tailed t-test of the hypothesis that attack rates were higher for birds that were near to another bird.

To assess resource dispersion, we performed a randomization test with our longest continuous observation of a focal individual. First we classified each 10-second time interval as 0 or 1 for low attack rates ($<$ median) or high attack rates ($>$ median), giving us a time series with an equal number of 0s and 1s. Then we calculated the frequency distribution of intervals (one or more 10-second periods) between each time of high attack rates and the nearest time of high attack rates. The test statistic was the median time

intervals between periods of high attack rates. We compared this test statistic from the empirical data to a frequency distribution of 10,000 such median intervals calculated with each 10 sec interval being randomly assigned as either high or low attack rates (following from the biological null hypothesis of random encounters of food items through time).

To record home ranges and foraging paths, we tracked nine additional groups using a GPS system during time-spans of 6 to 100 minutes on paths of 10 to 60 meters. We also recorded encounters between groups and the coordinates at which they occurred. We plotted waypoints to mark the beginning and end of sample groups, and used MapSource software to acquire and map the paths of finches.

RESULTS

We observed 20 flocks of between 2, 3, and 4 birds ($n = 12$, 2, and 4, respectively) for an average of 7 minutes per group. Each flock consisted only of adults (juveniles are easily distinguishable from adults by color and markings); 30% of groups that we observed contained more than 2 foraging adults.

Large-footed Finch attack rates were 2.29 times higher when they were near another finch ($t = 5.34$, $df = 88$, $P < 0.0001$; Fig. 1).

Neither attack rate nor proportion of time near another finch were related to group size (Regression $F < 0.42$, $df = 1, 91$, $P > 0.52$). Ten second intervals with high attack frequency were nonrandomly aggregated in time (Fig. 2; $P = 0.0004$ from randomization test).

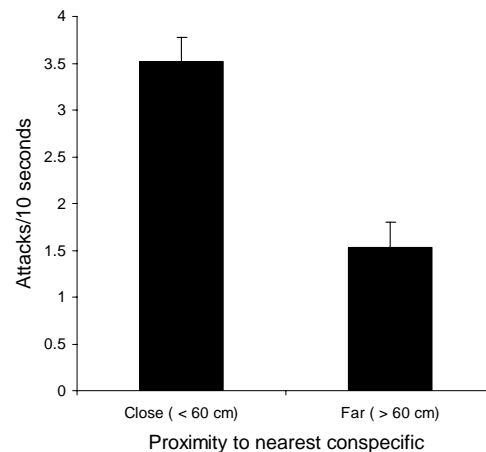


Figure 1. Mean attack rate (± 1 SE) for Large-footed Finch groups when one or more group members were near and far from nearest group member in Cerro de la Muerte, Costa Rica.

We were able to track the movements of nine flocks of Large-footed Finch for 2 to 65 minutes. Based on the GPS tracks (Fig. 3), they had a median foraging path of 30 meters for approximately 17 minutes, giving an average speed of 1.7 meters per minute. Flock movements involved frequent turning, rather than linear progress through the landscape (Fig. 3). Two of 9 group paths directly overlapped.

Our observations showed a surprising inconsistency in the nature of group encounters. Six

aggressive interactions between foraging groups resulted in individuals or pairs relinquishing foraging ground. In contrast, 5 groups merged and foraged together.

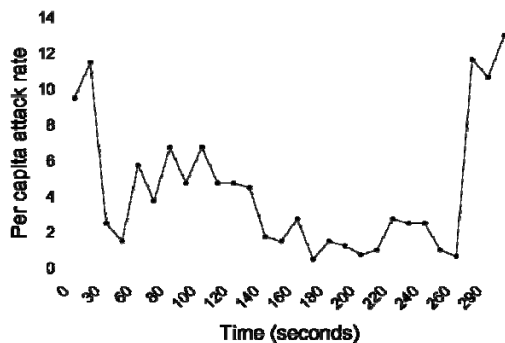


Figure 2. Number of attacks per 10 sec period by a Large-footed Finch that was observed continuously for 290 seconds at Cerro de la Muerte, Costa Rica.

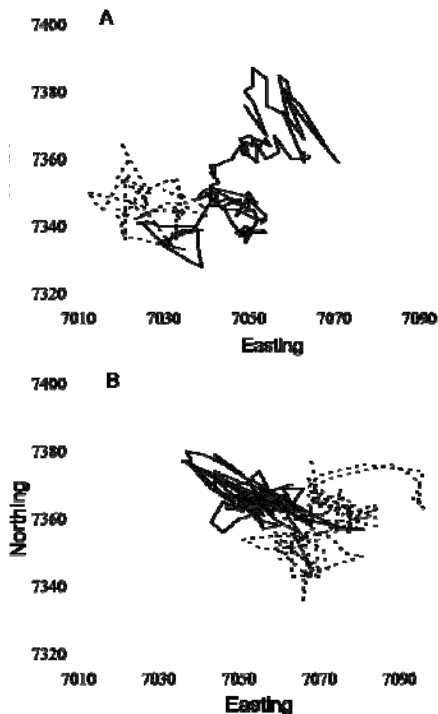


Figure 3. Foraging paths of Large-footed Finch groups at Cerro de la Muerte, Costa Rica. **A** two groups on 1 Feb, 2008; **B** two groups in same area on 2 Feb, 2008.

DISCUSSION

Large-footed Finches employ powerful double-scratches to expose seeds and insects in ground litter (Stiles and Skutch 1989), which may also be exploited by a near neighbor. Attack rates, which are presumably related to resource acquisition rates, averaged more than twice as high for birds that were within 60 cm of a foraging conspecific. This supported the hypothesis of increased foraging efficiency in groups. However, time spent in close proximity did not change with group size. Thus, it is beneficial to forage in a group, but groups of 4 are not obviously better than groups of 2 or 3.

The hypothesis that groups are favored by birds and not just accidental was further supported by our tracking data, which illustrated the stability of finch pairs. Though groups merged and broke apart with considerable fluidity, pairs stayed together throughout. We guess that the stable hunting pairs are also reproductive mates. So it is likely that there are benefits for them being together that go beyond impacts on foraging success.

Groups of all sizes showed aggregation of attacks in time, which indicated an aggregated dispersion of resources in space. This aggregation may also explain variation in the nature of group interactions. Aggregated resources may support larger groups of

finches, and eliminate the need to defend resources. Conversely, foraging in areas of local scarcity could explain the occurrence of aggressive behavior. In these areas, more intense competition for resources could encourage aggression between groups.

Regardless of resources, finches may benefit from being in larger groups if they decrease time spent being vigilant and increase time spent foraging. We did not collect data on predation or vigilance, so cannot support or refute this hypothesis. The possibility that finches form groups based on kinship and parental care is refuted by the absence of juveniles in larger groups, but juveniles might be a part of foraging groups at other times or places.

The erratic paths of finch foraging may increase efficiency of resource location by allowing finches to cover the most ground possible. Our tracking maps indicated that the finches have relatively small home-ranges, suggesting that there is a

large arthropod community present in the leaf litter at Cuerici, and that the replacement rate of prey is relatively high.

The high speed of finch foraging suggests that it is efficient for finches to cover more ground rather than to be very thorough in their foraging. This hypothesis is consistent with optimal foraging theory for patchy resources (Fig. 2) that are relatively easy for foragers to move among. It is also supported by the increased foraging success in groups. Apparently, individual finches do not scour prey from within patches of high food abundance. Their relatively small home ranges would be beneficial if they can become familiar with the local spatial patterns of prey availability.

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TOSSING PASSALIDS: EFFECTS OF SUBGROUP TRANSPLANTATION AND DISTURBANCE ON SOCIAL INTERACTIONS

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Abstract: Social behavior is uncommon in Coleoptera. A notable exception is the Passalidae, which live in social colonies, stridulate (potentially to communicate), and are reported to have parental care. We tested if parental care extends to protecting brood from disturbance. We collected groups (putative family groups beneath logs) of two passalid species in the high altitude forests of Costa Rica and studied their responses to laboratory simulations of disturbance. The coordinated defense hypothesis predicted that members of the same social group in both species would aggregate, and members from different groups would move away from each other in response to disturbance over time. We found no difference in the distance between members of the same or different social group or any signs of social interaction, suggesting that passalid social behavior degrades in the face of disturbance.

Key Words: Aggregation, coleoptera, colony, communication, sociality

INTRODUCTION

A subset of insect species, chiefly Hymenoptera and Isoptera, show social behavior such as parental care and coordinated movement. Additionally, Coleopterans are known to exhibit primitive eusocial behaviors (Brandmayr 1992). Passalid beetles (Scarabaeoidea) live in colonies in which adults and teneral (immature) adults cooperate in brood care of larvae, pupae, and eggs in rotting logs (Borror et al. 1963). However, little is understood concerning whether social group behaviors such as aggregation and parental care hold up under severe disturbances such as predators overturning their logs. Previous observations suggest

that adults have the capacity to defend their larvae, but this behavior may dissolve under direct threats to the colony.

Two species of passalid beetles inhabit the high elevation forests of Costa Rica, a larger species approximately 4.5 cm in length (species A) and a smaller 2.5 cm long (species B) (Whited et al. 2004). We assessed movement of passalid beetles from the same and mixed social groups using laboratory bioassays. This experimental setup made possible the manipulation of social groups and more standardized results than would have been possible in the field.

Adult passalids are reported aid immatures by repairing pupal cases, feeding larvae with macerated

wood pulp, and defending colonized logs from other passalid intruders (Schuster 1975b). Reciprocal stridulation occurs between adults and larvae, presumably for communication, but its function is not well understood. A large investment in larval care may extend to protection of larvae in the event of disturbance.

Given their apparent capacities for communication, we hypothesized that disturbance would invoke a strong social interaction among family members. From this we expected to see a coordinated escape response and/or reciprocal stridulation. We compared the social responses to disturbance of putative family groups with unrelated adults and larvae. This provided a test of whether social behavior is upheld in a mixed social group setting. If social behavior persists in these conditions, adults would move closer to larvae and adults of the same group over time, and away from members of another group.

METHODS

On the morning of 1 Feb 2008 we systematically searched for beetle-inhabited logs along the Mirador Trail in high elevation secondary forest of Cuerici, Costa Rica. We found eight discrete groups of passalids that contained at least one adult and one larva (4 groups

each of the large species and the small species). In the colonized logs, we noted the number of adults and larvae of either species. We then collected all adults and larvae for laboratory experiments, keeping each discrete social group (defined as all the individuals found on a single log) in its own bag.

We monitored each group's response to disturbance by creating a 1 x 1 m arena, with a thin soil layer and two oak logs (formerly inhabited by passalids) on either side. We "disturbed" each social group of each species by carefully handling them and gently placing ("tossing") groups into the center of the arena. We then tested each group after disturbance, measuring (every 1 min up to 5 min) the distance (in cm) among all individuals, and noting whether distances were adult to adult, adult to larva, or larva to larva. At every 1 minute interval we also recorded whether any individuals were engaged in any other escape behaviors such as digging or burrowing under a log.

We conducted a second experiment to test whether beetles of mixed social groups responded to disturbance in a similar manner as they did in their own social group. We conducted intraspecific trials to control for potential variation between species A and B. From each social group, we randomly paired one adult and one larva for study (referred to as 'pairs'). We then

tested for variations in aggregative behavior by measured mean adult-adult and adult-larvae distances in pairs from different social groups.

RESULTS

We searched 53 oak logs and found beetles within or beneath 15 of them. Seven were inhabited by the large species (11 adults and 15 larvae) and 8 by the small species (14 adults and 15 larvae). The two species did not co-occur in any logs.

When placed in the center of an experimental arena (simulated forest floor), the adults appeared to move away haphazardly, while the larvae barely moved, remaining within 5 cm of where they were placed in all trials. Adults from the same social group never relocated to opposite sides of the grid after five minutes (adults recruited to same side in 2 of 7 trials; in the other 5 trials, one stayed in center while the second hid under a log), whereas adults from different social groups relocated to opposite sides in 5 of 7 trials. However, there were not enough data to test whether this pattern was nonrandom. Some adults hid beneath one of the logs, while others burrowed in the soil in the middle or edge of the arena. We did not observe any stridulations or direct interactions between beetles.

There was no evidence that movements within an unfamiliar arena were coordinated within social

groups. Coordinated movements could have been evident as a tendency for individuals of the same social group to be closer to each other than to members of another social group. However, this was not true for either adult-larva distances (Fig. 1; $t = 0.19$, $df = 4$, $P = 0.43$, for paired t-test) or adult-adult distances (Fig. 2; $t = 0.89$, $df = 6$, $P = 0.21$).

Distances between conspecific individuals did not differ between species A and B (distance between adults from the same group: $t = -0.80$, $df = 6$, $P = 0.45$; adults from different groups: $t = 0.87$, $df = 5$, $P = 0.42$); adults and larvae from the same group: $t = 0.61$, $df = 12$, $P = 0.55$; and adults and larvae from different groups: $t = 0.41$, $df = 7.35$, $P = 0.69$].

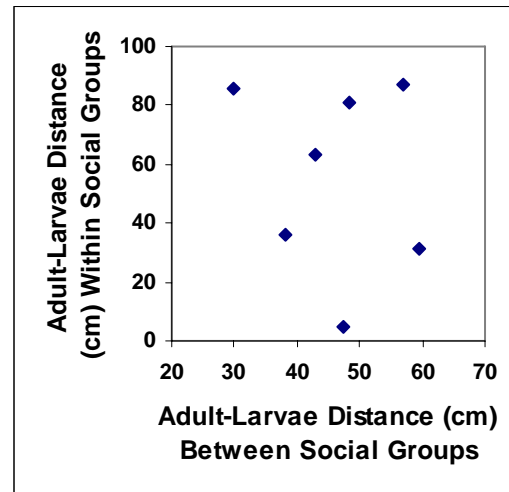


Figure 1. Comparison of the average distance between adults and larvae depending upon whether or not they were members of the same social group. Figure shows measurements five minutes after animals were placed together in the center of an unfamiliar arena. Seven individuals were tested (black = large species, grey = small species). Social groups of beetles were collected along the Mirador Trail behind the Estación Biológica, Cuerici, Costa Rica.

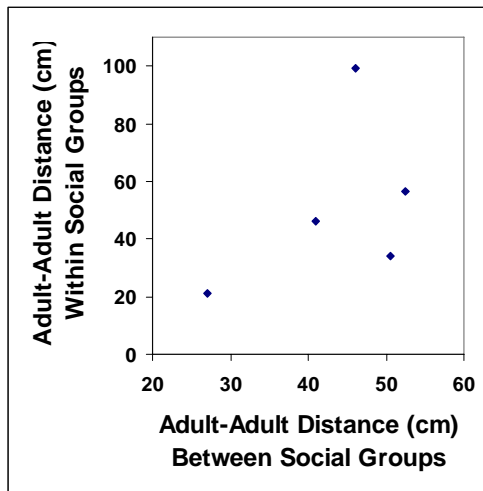


Figure 2. Mean distance between adults from the same social group (y-axis) and adults from different social groups (x-axis) five minutes after disturbance in two species of passalid beetles. Five individuals were tested (black = large species, grey = small species). Social groups were collected along the Mirador Trail behind the Estación Biológica, Cuerici, Costa Rica.

DISCUSSION

We found no indication that passalids influenced larval or other adults' behavior, irrespective of social group identity.

Beetles stridulated readily when we picked them up or poked them, but they never stridulated during our trials. If stridulating is a mode of communication among passalids, we would have expected to observe some degree of reciprocal stridulation, either between adults, as demonstrated in previous experiments (Close et al. 2002), or between adults and larvae.

The simple interpretation of our results is that passalids simply lack the social skills for a

coordinated escape response. However, another possibility is that it is adaptive for adults to abandon their young when the social group is disturbed. The life history of passalids at Cuerici is not known, but passalids in general are reported to produce brood at least annually, and to live as long as 14-16 months as adults. Therefore, they may have future reproductive opportunities even if they lose one brood, and the value of preserving future reproduction might exceed the benefits of trying to protect or shepherd their current brood. Also, it may be adaptive to disperse after a disturbance rather than aggregating into a larger prey target.

In contrast to some previous studies at Cuerici, we found passalid social interactions to be limited at best. Stork et al. (2006) suggested that disturbance may invoke a coordinated escape response in which adults aid larvae. In their studies, larvae that were discovered beneath logs in the morning had all disappeared by the afternoon, leading them to hypothesize that adults assisted in moving the relatively immobile larvae to another location. Our studies seemed to validate that the larvae have limited mobility, but we found no evidence of parent-assisted movements of larvae.

Passalids inhabit moist, dark logs, and it is possible that our experimental arena was too artificial

to reveal the natural tendencies of our study species to aggregate as social units. Alternatively, passalid aggregations might be better understood as the coincidental clumping of individuals within isolated habitat patches (oak logs) rather than socially structured family groups.

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THE TRADEOFFS OF TILTING: AN ANALYSIS OF NON-VERTICAL GROWTH IN A MONTANE TROPICAL FOREST

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Abstract: On steep forested slopes, trees could gather more light and reach the canopy faster if they grow non-vertically, so the benefits of tilt might outweigh its costs (such as increased risk of getting uprooted). Before the effects on tree tilt of environmental factors such as light availability can be meaningfully considered, it is necessary to know that tree tilt is an adaptive trait of the trees to their surroundings, and not a mere response to ground slope and gravity. To distinguish between these possibilities, I built a mathematical model of tilt, and tested it against real data from Cuerici. The cost-benefit model of tilt found that tilting should be more beneficial on steeper ground, and predicted that if tilting is adaptive, then shade intolerant species should show more tilt than shade tolerant species because they cannot survive in low light. I sampled twenty trees in the steep forest of Cuerici, and found no significant relationship between either ground slope or compensation point and tree tilt, but I did detect evidence that trees grow towards increasing light. These mixed results show that tree tilt is likely to be the result of both the physical constraints of growing on a slope and the remarkable plasticity of trees to adapt their shape to their environment.

Key Words: torque, compensation point, tapering, game theory, parameter space

INTRODUCTION

Reaching the canopy is critical to the survival and reproductive success of all canopy trees (Clark and Clark, 2001). On a steep slope, trees with unconstrained phototropic growth would be tilted so as to gather more light, and reach the canopy at a lesser height (Figure 1). However, tilted trees are subject to torque from gravity, which increases the risk that they will snap or get uprooted. As a result, tilting might come at the cost of additional wood for supportive structures (Leohle, 1986). Trees on slopes cannot simultaneously grow in such a way

as to maximize light and to minimize physical stress.

If the light gradient is non-vertical, then trees might benefit from growing such that they tilt their trunks in the direction of increasing light availability. Of course there is an alternative non-adaptive explanation that could explain tilted tree trunks. For trees growing on slopes, there is less downhill ground for supporting roots, and gravity acting on this asymmetry could force trees to be tilted. Understanding the causes and consequences of tilting tree trunks could help elucidate the effect of landscape topography on forest architecture.

I created a model to theoretically consider the cost and benefit of tilted growth. I explored the net effect (defined as benefit - cost) of tilt and calculated the optimal amount of it for any given ground slope. I compared net effect of tilt of shade tolerant and shade intolerant trees, and compared the model's predictions with real data from the hilly forest of Cuerici, Costa Rica.

If tilting is an adaptive trait (i.e., which produces a net benefit), then it should be optimized with respect to the life history of the tree. Shade tolerance is a variable trait that seems like it would matter to the optimization of trunk tilting; shade intolerant trees (high light compensation points) should tilt more than shade tolerant trees (low light compensation points) because the benefits of reaching the canopy are greatest for trees that are relatively shade-intolerant. Under the alternate hypothesis that tilting is a nonadaptive response to gravity, there should no relationship between light compensation point and tilt.

METHODS

Model formulation

To model the benefit and cost of tilt, I assumed that the benefit was proportional to the difference between the vertical and tilted lengths (noted 'C' and 'H') that the tree would have to grow to reach the

canopy, and that the cost was proportional to the torque incurred due to gravity. From these assumptions, I derived the following equations (see Appendix):

- (1) $B(\alpha, \beta) = \lambda \cdot C \cdot (1 - \cos(\alpha) / \cos(\alpha - \beta))$
- (2) $C(\alpha, \beta) = k \cdot C \cdot (\cos(\alpha) \cdot \sin(\beta) / \cos(\beta - \alpha))$

where α is the angle of the ground (relative to horizontal, Figure 1), β is the angle of the tree (relative to vertical), $B(\alpha, \beta)$ is the benefit function, $C(\alpha, \beta)$ is the cost function, k is the proportionally constant for cost (which itself is proportional to the mass of the canopy times the force of gravity), λ is the proportionality constant for benefit, and C is the height of the canopy (see Appendix).

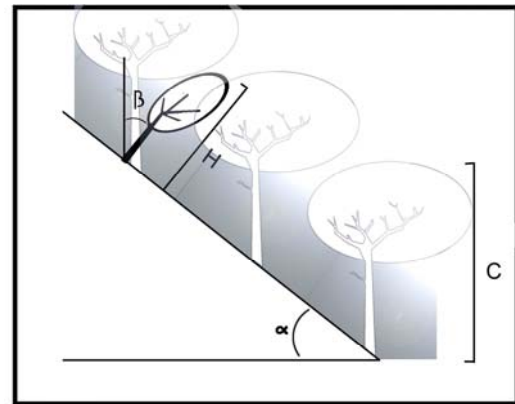


FIGURE 1. Graphic representation of the model parameters C , H , α , and β to investigate the effect of ground slope (α) on tree tilt (β).

I examined the shape of the benefit and cost functions, and explored parameter space in terms of α , β , and the λ/k ratio. Because trees with higher compensation points

need to reach the canopy faster, the benefits to tilt would be greater than those of trees with lower compensation points, while the costs would be roughly similar. Therefore, I compared the higher and lower compensation point groups by evaluating model behavior for each group with parameters set at $(\lambda, k) = (10,1)$ and $(\lambda, k) = (2,1)$, respectively.

Data collection

I sampled twenty large trees under the canopy on the hills of the primary forest of Cuerici, Costa Rica. I walked in a random compass direction for a random number of steps (< 100 steps), and then sampled the nearest tree of height greater than 7 m. For each tree, I estimated α by putting a piece of tape on the tree at eye-level, walking 3 meters downhill along the hill's gradient (i.e. the direction of steepest descent), and sighting the tape with a clinometer. I estimated the angle of the tree's tilt by resting the clinometer on its trunk at breast height (β_1) and measuring trunk tilt, and then standing next to the trunk and sighting the center of mass of the canopy (β_2). For every tree the estimated position of the center of gravity fell along the axis of the tree tilt, so β_1 and β_2 can be compared. Both β_1 and β_2 were square-root transformed to improve normality. I aligned myself with the hill gradient (i.e. the axis along which it rises most steeply) and recorded the hill aspect

(degrees relative to north), then aligned myself with the axis of the tree's tilt, and recorded the tree aspect. I estimated the alignment of the hill gradient and the tilt axis by taking the difference of these two aspects. I recorded the circumference of each tree at breast height and ground level, and estimated tree height, position in the canopy (dominant, co-dominant, intermediate, overtopped) and percent live crown by the ratio of height of first leafy branch to tree height.

The trees above the median percent live crown were assigned to the high light compensation point (shade intolerant) group and the rest were assigned to the low light compensation point (shade tolerant) group. To estimate tapering, I calculated the ratio of trunk cross sectional area at breast height relative to that at ground level. Finally, to estimate the relative strength of the tree's base, I calculated the ratio of trunk radius at ground level relative to tree height.

RESULTS

The model predicted that the benefit of tilt is maximized when $\beta = \alpha$ (i.e., when the tree is perpendicular to the ground), and increases with increasing α (Figure 2, top panel). The cost of tilt increased non-linearly with increasing β , and

decreased with increasing α (Figure 2, bottom panel).

Combining these two functions, and weighting the benefit and cost functions in two different ways showed increasing net benefit of tilt with increasing ground slope, and increasing optimal β with increasing α (Figure 3). Thus the model predicts little or no benefit from tilting at low ground slopes (small α values), but as α increases, tilting is predicted to become increasingly favored and optimal tilt is predicted to become more extreme relative to vertical as the ground slope increases. Finally, the model justified that higher compensation point trees should be more tilted, since they benefit more from tilt, and have higher optimal β values for a given ground slope (Figure 3, top panel).

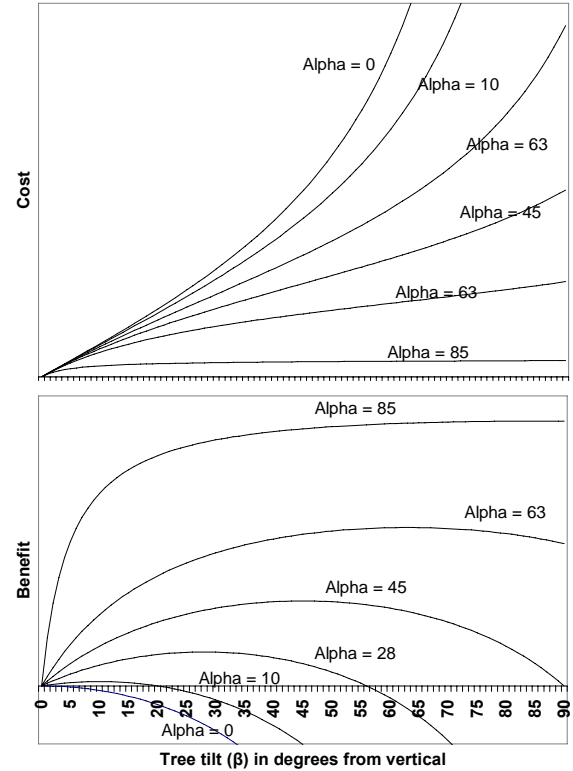


FIGURE 2. Estimated cost (top panel) and benefit (bottom panel) of tilted growth given by equations (1) and (2) for six fixed α values, where α is the angle of the ground relative to horizontal, and β is the angle of the tree relative to vertical.

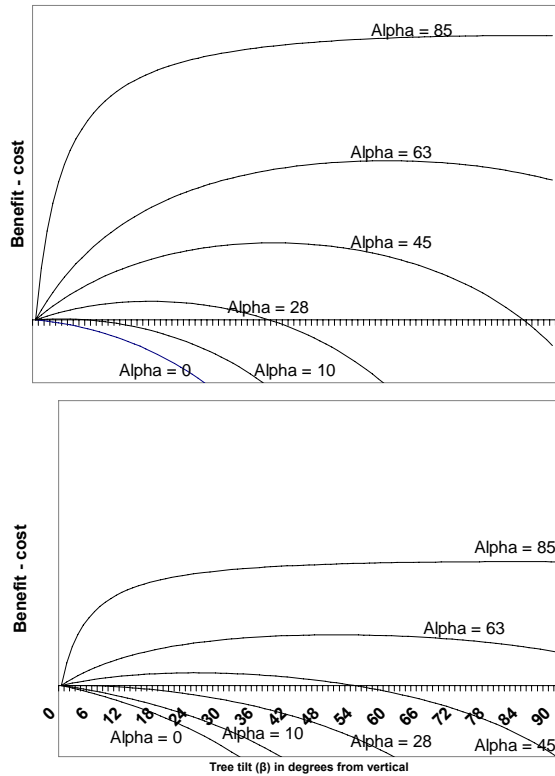


FIGURE 3. Cost-benefit analysis of tilted growth as given by $B(\alpha, \beta) - C(\alpha, \beta)$ from equations (1) and (2) for six fixed α values, where α is the angle of the ground relative to horizontal, and β is the angle of the tree relative to vertical. The top panel represents $(\lambda, k) = (10, 1)$ to simulate high compensation point trees, while the bottom panel represents $(\lambda, k) = (2, 1)$ to simulate low compensation point trees. Positive values indicate that the model predicts a net gain given these parameters.

In the primary forest of Cuerici, ground slope was clearly related to tree growth form: e.g., large trees (>7m in height) were off vertical by mean \pm SE = $10.9 \pm 10.5^\circ$, and all the trees tilted downhill: mean aspect difference \pm SE = $12.2^\circ \pm 30.0^\circ$; $t = -23.8$, $df = 17$, $p < .0001$; t -test based on the expected mean (by the law of large numbers) of 180° if the two aspects were independent of one another).

However, several other results were contrary to that predicted by the model. There was not a strong relationship between ground slope and tree tilt ($F = 1.07$, $df = 1, 18$, $p = 0.31$, Figure 4). There was no significant difference in tilt between trees classified as having the low and high compensation points ($t = 1.24$, $df = 18$, $p = 0.23$).

There was no relationship between tilting and tapering ($F = 0.81$, $df = 1, 18$, $p = 0.38$) or tilting and base strength ($F = 1.18$, $df = 1, 18$, $p = 0.29$). Canopies were asymmetrical, and were larger downhill: comparing β_1 and β_2 showed that the center of gravity of the canopy was significantly further downhill than would be expected given the tilt at the base of the tree (paired- $t = 1.86$, $df = 18$, $p = 0.04$).

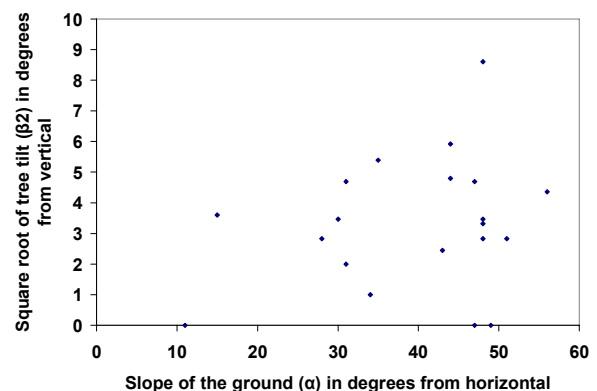


FIGURE 4. Scatterplot of tree tilt (β_2) by ground slope (α) of twenty trees in the forest of Cuerici, Costa Rica.

DISCUSSION

In general, model predictions regarding the effect of ground slope and light compensation point on tree tilt were not supported by the data. This could be due to some of the model's assumptions (e.g., for large β values the cost remains proportional to torque) or simplifications (e.g., it does not account for tree age, which should correlate with canopy mass and affect k). Despite these limitations, the model provided a structured theoretical investigation into the effects of ground slope and tree tilt on optimal growth, and it would become more valuable if future studies could estimate the parameters λ and k .

The data did not support the hypothesis that the cost of tilt would be visible in the tapering and larger basal area of the trunk. Root density and risk of getting uprooted are probably more correlated with tilt, and would reflect its true cost. The result that compensation point did not affect tilt is inconsistent with it being an adaptive, optimized trait. However, this was not a robust result because the compensation point data were based on rough estimates within a small range of low compensation points (all the study trees were quite shade tolerant). Furthermore, it might be impossible to sample trees with a high compensation point growing under

the canopy (which would be necessary to avoid introducing confounding variables) since such shade intolerant trees are unlikely to survive there. Yet, it has been shown that canopies become more developed in regions of greater light (Leohle, 1986), and I found that tree canopies extended farther downhill. This is consistent with the highest light availability being in the direction in which a tree tilts, as would be expected if tilting were adaptive.

If tilting is indeed adaptive, then its long term dynamics could be analyzed with game theory. The optimal amount of tilt in this study was calculated based on the assumption that most canopy trees are vertical. But as more trees become tilted to optimize light, the benefit function would slowly change shape, and it would become more advantageous to grow vertically again. The rate at which this shift happens would determine the stability of the state of dynamic equilibrium between tilted and vertical tree populations.

LITERATURE CITED

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APPENDIX: MODEL DERIVATION

$$H = C \cos(\alpha) / \cos(\beta - \alpha)$$

$$\text{Benefit} = \lambda (C - H)$$

$$\text{Cost} = F \times d \cdot k$$

$$= k \cdot H \cdot \sin(\beta)$$

$$= k \cdot C \cos(\alpha) / \cos(\beta - \alpha) \cdot \sin(\beta)$$