

on the alluvial fan are notoriously poor in organic matter, and even recently could be cultivated only with the intensive ploughing in of manure and crop stubble.

The approximate date of AD 719 thus marks a time when the Tarata waterworks were already functioning, although 3,500 yr BP is an estimate of its earliest use. Unfortunately the preceramic and early ceramic periods of the Cochabamba highlands are virtually unknown¹⁷. Remains of palaeo-canals, such as one located 50 m downstream of the Gringo Canal offtake, suggest a wealth of material for archaeological research (Fig. 1). Shard fragments found with the charcoal-bearing lens of the P-11 site indicate that by AD 719 irrigated fields were probably being used occasionally as sites of cooking and perhaps even short-term habitation, as they are in the present-day farming systems of Quechua- and Aymara-speaking peasants.

The extensive system of floodwater-canal irrigation at Tarata offers a new perspective on early Andean waterworks. It demonstrates that later civilizations such as the Tiwanaku and Inka Empires could tap a mountain-based mastery of controlling floodwater and engineering canals. A legacy of expertise would have contributed to their rapid expansion of water control and management. Hybrid arrangements, such as Tarata, were probably an important transitional stage in the evolution of Andean irrigation from rudimentary floodwater farming without canals to the full-scale canal irrigation that was typical of the later empires and chiefdoms. Finds at Tarata suggest parallels with the early history of irrigation in the coastal and low inter-Andean valleys of western South America, where farmers adopted irrigated farming by 3,500 yr BP^{17–20}.

Evidence of early irrigation at Tarata also explains the long-term use of environments and agricultural resources in the Andean uplands. Tarata's irrigation system offers the most specific evidence so far of how various world-renowned Andean crops could be cultivated before Inka rule in the widespread and heavily populated semiarid and subhumid environments that cover intermediate elevations between 2,000 and 3,500 m (refs 21, 22). Only early irrigation, exemplified by the Tarata works, could

have made possible the expansion of farming and the culture of diverse crops in the important intermediate-elevation habitats of the tropical Andes mountains. □

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Alternative antipredator defences and genetic polymorphism in a pelagic predator–prey system

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DIET vertical migration (DVM) of zooplankton is generally considered to be a predator-avoidance strategy: zooplankton migrate to greater depths during the day to reduce their chance of being detected by visual predators (fish)¹. Both phenotypic plasticity and interpopulational genetic variability in DVM patterns exist in zooplankton^{2,3}. We used large indoor mesocosms ('plankton towers'⁴) to study intrapopulational genetic variation for day depth

in a *Daphnia hyalina* × *galeata* hybrid population. Clones differing in body size also differed in vertical distribution, with the largest clone residing at the greatest depth during the day. A selection experiment in the presence of fish indicates that alternative antipredator strategies, which involve a complex association between habitat-selection traits and life-history strategies, might be an important factor underlying intrapopulational genetic polymorphism in zooplankton, through a balancing of fitness effects in the presence of visual predators.

Predation is often important in the structuring of communities and populations^{5,6}. Although theoretical studies^{7,8} have attempted to model the impact of predation as a selective force influencing genetic variability in prey populations, there have been few empirical studies of the direct impact of predation on the genetic composition of prey populations^{5,9}.

Diel vertical migration (DVM) of zooplankton is generally considered to be a strategy to reduce vulnerability to visual predators^{10,11}. All else being equal, larger zooplankton individuals should reside at greater day depths than smaller individuals. This has been observed repeatedly in comparisons of ontogenetic stages of a given species^{12,13}, in intraspecific^{14,15} and interspecific comparisons¹⁶.

It has been shown that DVM in zooplankton can be induced by the presence of predator-specific chemicals^{2,17,19}, but there is substantial evidence of genetic polymorphism for vertical migration behaviour, at least in the freshwater cladoceran genus *Daphnia*^{13,20,21}. In laboratory studies, *Daphnia* clones that inhabit shallow day depths²² mature at smaller sizes than clones that

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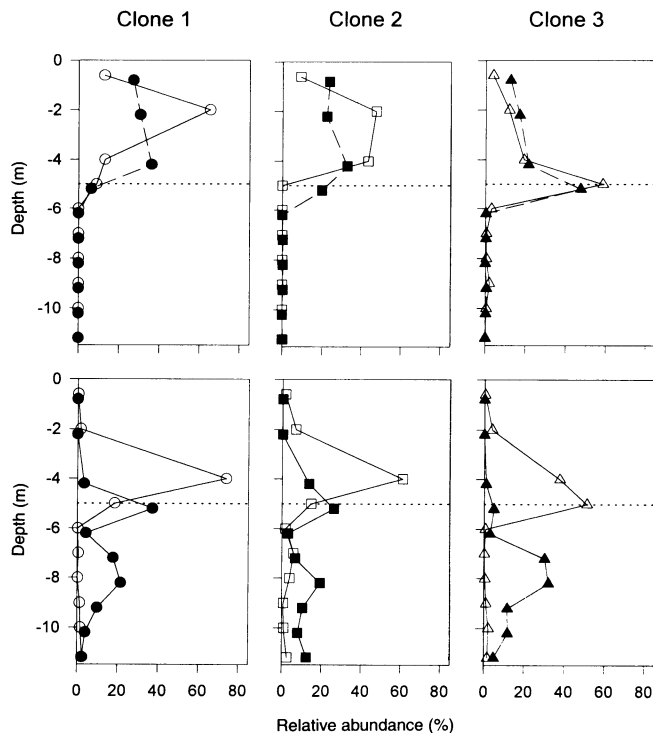


FIG. 1 Vertical distribution of three *Daphnia hyalina* × *galeata* clones in the plankton towers. Top, average vertical distribution of adult females during day (open symbols) and night (filled symbols) in the absence of fish chemicals or fish ($n=4$ sample series). Bottom: daytime distribution in the presence of fish chemicals (open symbols; $n=9$) and fish (filled symbols; $n=13$). The dotted line indicates depth of thermocline. The plankton towers are large (11.2 m high, cross-section 0.86 m), indoor, twin tower-tank systems⁴. To mimic summer stratification conditions in a temperate lake, a thermocline was established at a depth of 5 m in both towers (epilimnion, 20 °C; hypolimnion, 8 °C). The epilimnion was gently circulated vertically, and food (the unicellular alga *Scenedesmus acutus*) was added daily to a final concentration of 0.8–1.0 mg C l⁻¹ in the epilimnion (daily feeding was stopped on day 39). At the start of the experiment, both towers were stocked with a mixed population of three naturally coexisting *D. hyalina* × *galeata* clones at a density of 1,000 adult females per clone per tower. All three clones were isolated in July 1994 from the Schöhsee (Plön, Germany) and grown as clonal populations in the laboratory. They were chosen because they could be distinguished by their electromorph patterns²⁷ at the *PGM* locus, and because they differed in their life histories and vertical distribution (L.D.M. & L.J.W., manuscript in preparation). From day 8 until day 15, one of the towers (day 8–12, tower 2; day 12–15, tower 1) received fish chemicals (10 *Leucaspis delineaatus* in a 60-l tub with continuous water flow to the tower and back), while the other tower served as non-fish control¹⁸. From day 15 onwards, both towers received fish chemicals. On day 24, 10 *L. delineaatus* (size 3–4 cm) were released into tower 1. On day 27, 50 *L. delineaatus* (size 2–4 cm) were released into tower 2. During the sampling bouts (during the day at 12:30 and night at 22:30), *Daphnia* were collected simultaneously at depths of 0.6, 2.0, 4.0, 5.0, 6.0, 7.0, 8.0, 9.0, 10.0 and 11.0 m, using pumps and flow-through traps⁴. If available, 40 adult females were analysed from each epilimnetic and metalimnetic depth, and 20 from each hypolimnetic depth. Individuals ($n=8,500$) were measured and their clutch sizes recorded, and they were frozen for electrophoresis²⁷. Overall, there are significant differences in average depth between clones 1 and 3 during the day, between all three genotypes during the night, and between day and night samples of each of the three clones (Wilcoxon, $n=24-26$, $P<0.01$, Bonferroni correction²⁸).

reside deeper during the day²³. There is a positive correlation between adult body size and number, size and starvation resistance of offspring^{24,25}. Larger individuals are, however, more vulnerable to visual predation than smaller ones. Migrating to greater depths during the day can reduce vulnerability to visual predation, but it entails a metabolic cost¹¹. As a result of these

conflicting pressures, multiple optima may exist, with non-migrating small individuals (or clones) and larger individuals (or clones) that migrate to greater depths during the day having essentially equal fitnesses.

We tested the hypothesis that differences in day depth might compensate for differences in body size with respect to the persistence of different clones under visual predation. To do this we monitored changes in clonal frequencies in mixed populations before and after the introduction of fish. Mixed populations of three naturally coexisting *Daphnia hyalina* × *galeata* hybrid clones, isolated from the Schöhsee (Germany) and characterized by a different size at maturity, were established in large, indoor, plankton towers (Fig. 1). The clones exhibited different vertical distributions in the towers, with the largest clone residing deeper in the water column than the two smaller clones (Fig. 1). During the day and in the absence of fish chemicals, most adults of clones 1 and 2 were found at 2–4 m, whereas most adults of the largest clone, clone 3, were observed at 5 m (near the thermocline). Clones 1 and 2 were distributed throughout the epilimnion during the night, whereas the vertical distribution of clone 3 did not differ appreciably between day and night. In the presence of fish chemicals, and after stocking the towers with fish, adults of clone 3 tended to reside deeper than those of the other two clones (Fig. 1).

Adults of clone 3 were larger on average than those of clones 1 and 2 (Fig. 2a). However, even though clones 1 and 3 differed

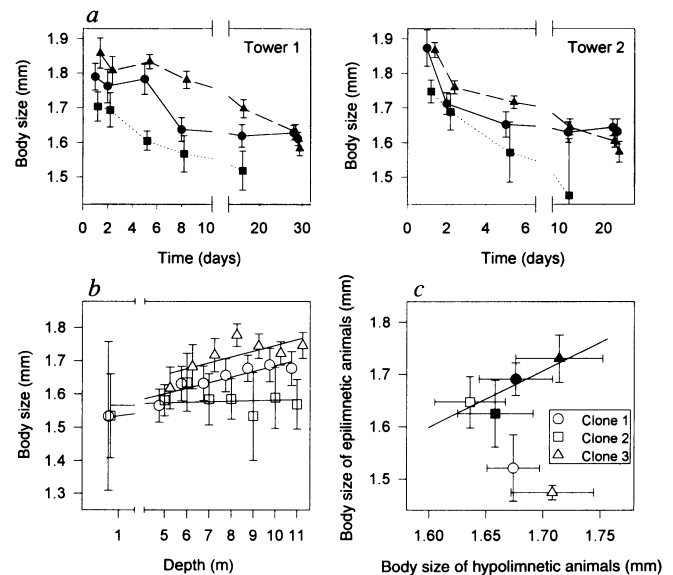


FIG. 2 Body size of clones 1 (circles), 2 (squares) and 3 (triangles) in the plankton towers. a, Changes in mean (± 2 s.e.) size of adult females of the three clones in the plankton towers after the addition of fish (day 1 was the first day with fish present). b, Mean (± 2 s.e.) body size of adult females of the three clones plotted against the depth at which they were caught. Pooled daytime samples from both towers, taken on three successive sampling days in the presence of fish; few individuals of clone 1 ($n=3$) and clone 2 ($n=9$) were caught in the epilimnion, and none of clone 3 were detected. These data were grouped into three depth strata (epi- plus metalimnion, 0–5 m; upper hypolimnion, 6–7 m; and lower hypolimnion, 8–11 m). Slopes in clones 1 and 3 are homogeneous ($P=0.999$), whereas the slopes are heterogeneous ($P=0.013$) when clone 2 data are included (ANCOVA). c, Mean size (± 1 s.e.) of adults in epilimnion plotted against size of adults in the hypolimnion, for day (open symbols) and night (filled symbols) samples. Clonal means were calculated using mean epilimnetic or hypolimnetic values for a given sample series (with values only included if based on 10 or more animals; $n=4$ series for daytime epilimnetic individuals for all three clones and night-time hypolimnetic clone 2; $n=7-11$ series for all other data; large error bars are due to changes in body size with time; see Fig. 2a). The line connects points of equal epi- and hypolimnetic body size.

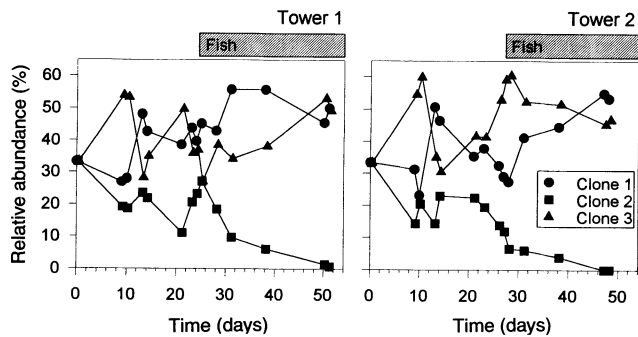


FIG. 3 Relative abundance (based on night-time sample series) of clones 1 (circles), 2 (squares) and 3 (triangles) in the two plankton towers. Frequencies (0.333) were equal at the start of the experiment. The shaded bars above the graphs show when fish were present. Birth rates²⁹ were calculated for a short period after fish were added (day 28–30), and were compared with estimates of r obtained from population growth rates during the same period. Approximately 1,700 and 500 *Daphnia* per fish per day were eaten in towers 1 and 2, respectively.

substantially in size, they both showed a very similar relationship between size and depth: adults of these clones that ventured into the epilimnion during the day were invariably small (Fig. 2b). During the day, adults of clones 1 and 3 that remained in the epilimnion were much smaller than animals of the same clones that resided in the hypolimnion (Fig. 2c; there were no size differences between epim- and hypolimnetic animals during the night). For clone 2 there was no such difference in size between epilimnetic and hypolimnetic individuals (Fig. 2c). As a result, the average size of the epilimnetic adult females during the day was larger for clone 2 than for the other clones, even though clone 2 was the smallest clone on average (Fig. 2a).

Overall, changes in clonal frequencies were similar in both towers (Fig. 3). Before fish were added the relative abundances of clones 1 and 3 converged at around 40%, with the relative abundance of clone 2 being about 20%. After stocking the towers with fish, the relative abundance of clone 2 (the only clone where large animals remained in the epilimnion during the day) was gradually reduced until near-extinction (0% in tower 2, and <1% in tower 1), whereas clones 1 and 3 continued to coexist, being at frequencies of approximately 50% at end of the experiment (Fig. 3).

We conclude that clones 1 and 3, which differ strongly in both DVM and life-history strategies, have similar fitnesses in the presence of planktivorous fish. Clone 2 may represent a third strategy, with individuals relying on their small size to remain longer in the metabolically more profitable epilimnion. In our experiment, clone 2 clearly had a lower fitness than the other two clones. However, in natural environments the relative fitness of clones with different migration strategies might depend critically on predation pressure and lake stratification. Under lower predation pressure than that established in the towers, it might be advantageous to remain in the epilimnion, irrespective of body-size characteristics.

This study shows that an association between behavioural (habitat selection) and life-history traits may result in alternative strategies, which in turn result in equal fitnesses for different genotypes when exposed to predation pressure. Such a balancing of fitness effects can perhaps explain the maintenance of genetic polymorphism for DVM in *Daphnia*, and possibly other zooplankton as well. More generally, our results illustrate the context under which complex strategies can evolve, and might provide a mechanism to promote the coexistence of genotypes in natural populations²⁶. □

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Insertions and duplications of mtDNA in the nuclear genomes of Old World monkeys and hominoids

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USING oligonucleotide primers designed to match conserved regions of mammalian mitochondrial DNA (mtDNA)¹, we have amplified and sequenced two divergent cytochrome *b* nuclear pseudogenes from orangutan cellular DNA. Evolutionary analysis suggests that a nuclear transfer occurred about 30 million years ago on the lineage leading to the catarrhines (Old World monkeys and hominoids), and involved a long (at least 3 kilobases), probably damaged, piece of mtDNA. After this transfer, the pseudogene duplicated, giving rise to the two copies that are probably present in all hominoids, including humans. More recent transfers involving the entire cytochrome *b* gene have also occurred in the Old World monkeys. Such nuclear copies of mtDNA can confound phylogenetic and population genetic studies^{2–4}, and be an insidious source of DNA contamination of ‘ancient’^{3,5} and forensic DNA. Indeed, contamination with these anciently transferred human pseudogenes⁵ is almost certainly the source of the cytochrome *b* sequences recently reported from ‘dinosaur bone DNA’⁶.

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