process Z_t starting from $Z_0 = 2$, using the values τ_0 and α_0 of τ and α estimated from the data as the parameters in each run. Paths in which either branch dies out before time T are excluded from the analysis. For each accepted run, i, we re-estimate τ and α, getting values $\tau_i, \alpha_i, i = 1, \ldots, b$. Run i also produces a value X_i^2 of the statistic in equation (5). Assuming[27] that the values of $\tau_i - \tau_0$ mimic the distribution of $\tau_0 - \tau$, we obtain a bias-corrected estimate of τ of $2\tau_0 - \bar{\tau}$, where $\bar{\tau}$ is the sample average of the replicates $\tau_1, \ldots, \tau_b$. An approximate $100(1 - 2v)\%$ equal-tailed confidence interval for τ is then given by $(2\tau_0 - \tau_{(b(1-v))}, 2\tau_0 - \tau_{(bv)})$, where $\tau_{(j)}$ is the jth largest of $\tau_1, \ldots, \tau_b$. We used $b = 2,500$. A similar method is used to find an upper 95% confidence interval for α and the α_j. The empirical distribution of X^2 can be found from the values of $X_1^2, \ldots, X_b^2$.

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Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years

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Historical catch records suggest that climatic variability has had basin-wide effects on the northern Pacific and its fish populations, such as salmon, sardines and anchovies[1–7]. However, these records are too short to define the nature and frequency of patterns. We reconstructed ~2,200-year records of sockeye salmon abundance from sediment cores obtained from salmon nursery lakes on Kodiak island, Alaska. Large shifts in abundance, which far exceed the decadal-scale variability recorded during the past 300 years[1–8], occurred over the past two millennia. A marked, multi-centennial decline in Alaskan sockeye salmon was apparent from ~100 BC to AD 800, but salmon were consistently more abundant from AD 1200 to 1900. Over the past two millennia, the abundances of Pacific sardine and Northern anchovy off the California coast, and of Alaskan salmon, show several synchronous patterns of variability. But sardines and anchovies vary out of phase with Alaskan salmon over low frequency, which differs from the pattern detected in historical records[5,6]. The coherent patterns observed across large regions demonstrate the strong role of climatic forcing in regulating northeastern Pacific fish stocks.

Salmon are important ecological, economical and cultural resources in the northern Pacific region, and their response to future climatic change is very uncertain[9]. Long-term relationships between sockeye salmon populations and climatic change can be evaluated by analysing sediment cores from their nursery lakes[8]. After one to four years of feeding in the northern Pacific, sockeye salmon (*Oncorhyncus nerka*) return to their natal lake/stream system to spawn and die[10]. The nutrients derived from spawned carcasses can be significant relative to other sources, and may be reconstructed from palaeolimnological records of $\delta^{15}N$ and algal bioindicators, such as diatoms[8]. Periods of greater input of salmon-derived nutrients (SDN), and hence greater sockeye salmon abundance, corresponded to higher sedimentary $\delta^{15}N$ and more eutrophic diatom taxa. Here we show reconstructions of salmon abundance over the past two millennia from lakes on Kodiak island, Alaska (Fig. 1), where our proxies have been successfully calibrated with monitoring data[8]. This region is one of the most important salmon-producing areas of the northern Pacific, and historical records suggest that its salmon abundances are representative of population trends in Alaska[4].

In Karluk lake (57° 25′ N, 154° 05′ W), our sedimentary indicators of SDN—$\delta^{15}N$ and diatoms—show striking changes and a strong degree of coherence ($r^2 = 0.79$, $n = 100$, $P < 0.001$) over the past ~2,200 years (Fig. 2). In the oldest sediments, around 200 BC, we infer from the high $\delta^{15}N$ values and the strong presence of mesotrophic to eutrophic diatom taxa (for example, *Stephanodiscus minutulus/parvus*) that the return of sockeye salmon to Karluk lake was high, and similar to levels (~3 million yr^{-1}) present when

commercial fishing began at the Karluk estuary in AD 1882 (ref. 8). A striking feature of the record is the dramatic and sustained change to lower SDN loading beginning at ~100 BC, as inferred from a shift in the diatom community to an oligotrophic assemblage (that is, a change in dominants to *Cyclotella comensis* and *C. ocellata*) and the strong decrease in $\delta^{15}N$. Beginning at about AD 250, there is a general

increase in $\delta^{15}N$ and an increase in oligo- to mesotrophic diatom taxa (for example, *Cyclotella pseudostelligera* and *Fragilaria crotonensis*), but peak abundance in SDN is not reached until ~AD 1200. Overall high levels of SDN are inferred for the period AD 1200–1900, with decadal-scale shifts as the main source of variability during this portion of the record. Declines in SDN since the 1900s can be
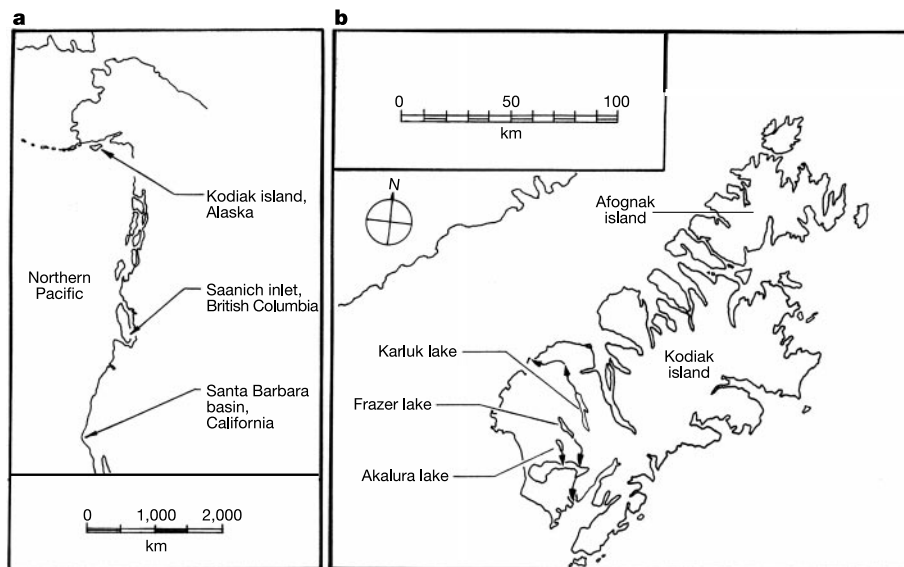

Figure 1 a, Map of the northeastern Pacific coast from Alaska to California, highlighting Kodiak island (this study), Saanich inlet[27] and the Santa Barbara basin[18,19,25]. **b**, Map of Kodiak Island showing Karluk, Akalura and Frazer lakes. That these lakes drain to different

parts of the island reinforces the concept that the $\delta^{15}N$ pattern reproduced in Karluk and Akalura lakes is not caused by tectonic processes.
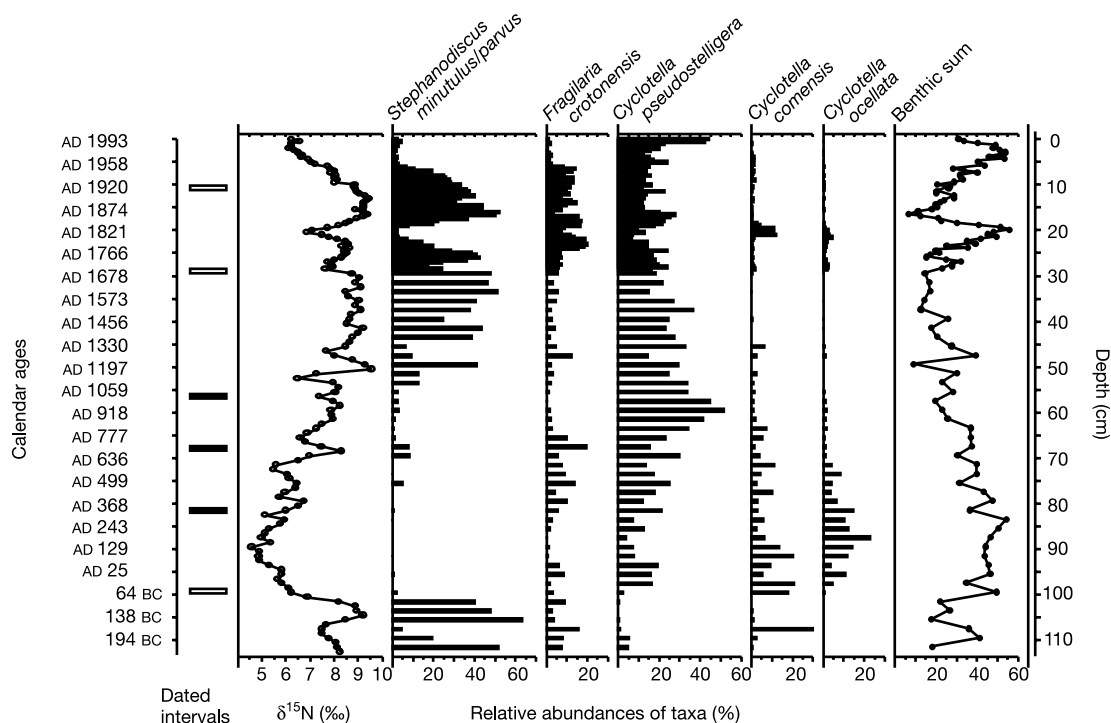

Figure 2 Palaeolimnological evidence of dramatic changes in sockeye salmon abundances from Karluk lake over the past ~2,200 years. As salmon transport significant quantities of nutrients enriched in $\delta^{15}N$ relative to terrestrial sources, high $\delta^{15}N$ values and the strong presence of *Stephanodiscus minutulus/parvus* (a mesotrophic to eutrophic indicator) reflect phases of large returns of sockeye salmon to Karluk lake. In contrast, periods of lower salmon-derived nutrients are marked by low $\delta^{15}N$ values and oligotrophic

(that is, *Cyclotella comensis* and *C. ocellata*) and benthic taxa[8]. Intermediate salmon-derived nutrient conditions are indicated by *C. pseudostelligera* and *Fragilaria crotonensis* (which have been shown to be responsive to moderate lake fertilization in Pacific coast lakes)[8,29]. The age model for this record was derived from dated tephras (white bars) and calibrated ^{14}C dates (black bars).

attributed to commercial fishing and climatic changes[8].

Direct impacts of climatic changes, and local landscape changes resulting from volcanism, tectonic activity and fires, can be ruled out as the primary sources of variability in the Karluk lake record. The volcanic ash layers are relatively thin (<1 cm) and significantly lag δ^{15}N and diatom changes. Tectonic processes can be ruled out on the basis of palaeoseismicity studies that suggest this region is subsiding, not uplifting, which would be a mechanism more likely to restrict access to the lakes[11]. The lack of a strong response in our nearby reference lake, Frazer lake (57° 15′ N, 154° 08′ W), over the past ~2,200 years suggests that the direct effects of climatic change (independent of sockeye salmon population fluctuations) were not the primary factors influencing Karluk lake. Frazer lake is very similar to Karluk lake, but has a steep waterfall at its outlet, which naturally prohibited salmon migration. It was not until the 1950s, when eggs were planted and a fish ladder was constructed, that a self-sustaining sockeye salmon run was established in Frazer lake[12]. Therefore any changes evident in the Frazer lake palaeolimnological record before the 1950s would reflect only climatic and landscape shifts. However, the δ^{15}N signature of Frazer lake is low and shows little variation over the past ~2,200 years, as would be expected for a reference lake with no influence of SDN (Fig. 3). Diatom analysis of these sediments also reveals only subtle variation and reflects constant oligotrophic conditions, consistent with no introduction of SDN. The greatest changes in the Frazer lake δ^{15}N and diatom records are associated with the introduction of sockeye salmon in recent decades[8].

The sustained multi-centennial regimes of anomalous salmon abundance, unprecedented during the historical period or during our short-te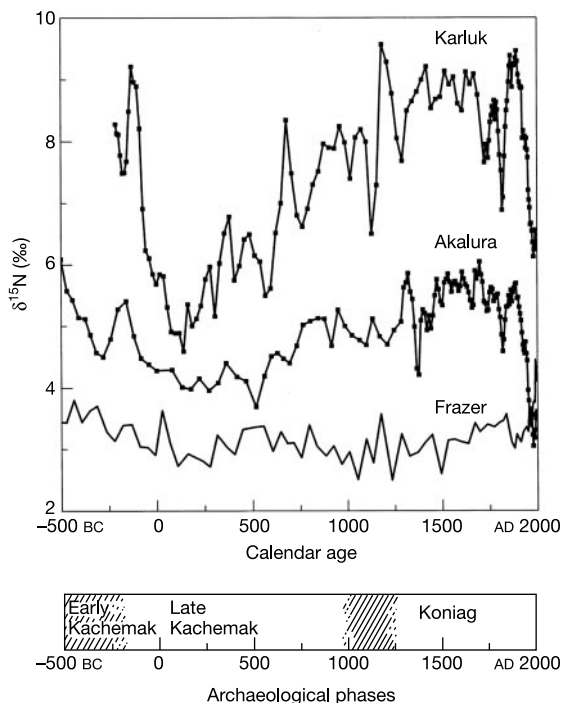rm 300-year records[8], appear to be regional phenom-ena, because a similar pattern to that seen in Karluk lake is observed in a second sockeye nursery lake, Akalura lake (57° 11′ N, 154° 12′ W; Fig. 3). The reconstructed patterns of salmon abundance also have strong similarities to changes in cultural characteristics and population estimates determined from archaeological data from Kodiak island. The abrupt reduction in SDN at ~100 BC appears to coincide with a major cultural change associated with the transition from the early to late Kachemak period[13] (Fig. 3). Subsequently, the increase in SDN from AD 800 to AD 1200 matches the change from the late Kachemak to the transitional Koniag and Koniag periods, when population numbers rose and a strong shift towards high utilization of salmon fishing gear is evident[14]. These archaeological data suggest that natural variability in salmon abundance influenced human culture, which differs from what has been observed in the twentieth century[8], and in other fisheries[15], where anthropogenic fishing has been an important determinant of coastal marine fish production.

Analysis of salmon catch records since the 1920s (refs 1–5, 7) strongly suggest that physical changes in the north Pacific Ocean are an important control on salmon production. Monitoring of primary and secondary production in the northeastern Pacific[16,17]

Figure 3 A regional comparison of sedimentary δ^{15}N profiles and the archaeological phases[10] from Kodiak island, Alaska. Both Karluk and Akalura lakes are natural sockeye salmon nursery lakes. Frazer lake, our reference lake, was without sockeye salmon until the 1950s (when it was stocked and a fish ladder was constructed) because it has an impassable waterfall at its outlet. The importance of changes in sockeye salmon abundance to the indigenous peoples of Kodiak is reflected in archaeological deposits[14] and the delineation of cultural phases[13]. A shift towards greater abundance of fishing tools[14], greater housing densities and larger multi-room houses is evident during the Koniag phase[14,30].
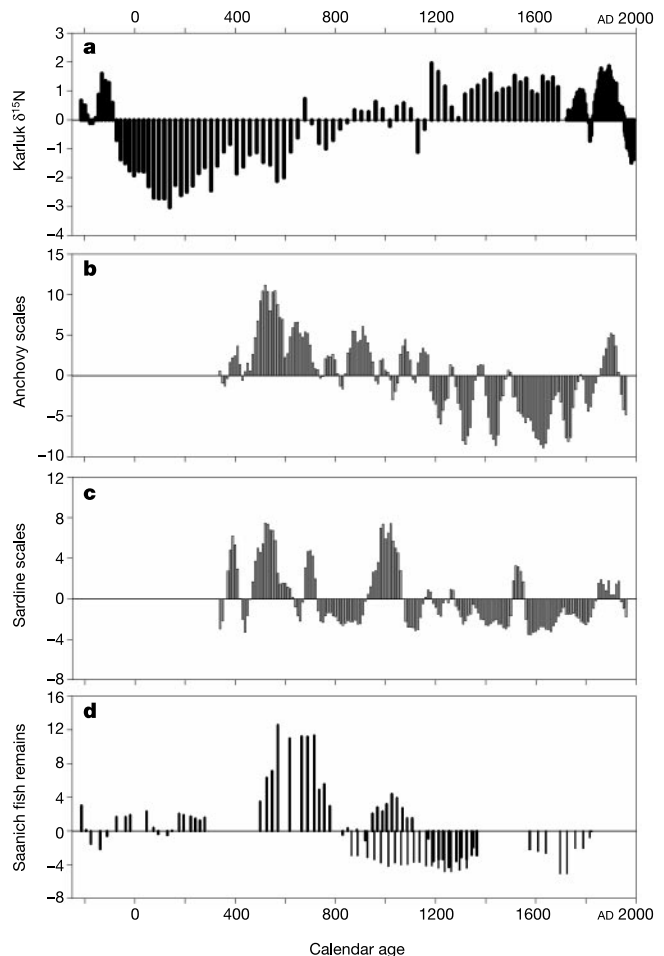

Figure 4 Reconstructions of fish abundances for the northeastern Pacific Ocean over the past ~2,200 years. Each series is plotted as the difference from the series mean calculated over the time period presented. **a**, The Karluk lake δ^{15}N profile (‰) as a proxy for sockeye salmon abundances in Alaska. **b**, **c**, Northern anchovy and Pacific sardine scales (no. of scales per 1,000 cm² per year) from the Santa Barbara basin, California[25]. A 50-year running average was applied to highlight long-term trends. **d**, Fish remains (including Pacific herring, Pacific hake and cartilaginous fish) (no. of fish remains per 100 cm³) recovered from Saanich inlet, British Columbia[27]; data from two overlapping cores are presented.

indicates that climatic forcing has a direct impact on lower trophic levels, which subsequently affects salmon production[4]. Historically, significant changes in states of northern Pacific fish populations and climate have occurred over interdecadal-scale periods[1–7]. However, our long-term data reveal the existence of longer multi-centennial regimes. The two noticeable multi-century shifts in inferred sockeye abundance at ~100 BC and ~AD 800–1200 correspond to periods of major change in ocean–atmosphere circulation in the northeastern Pacific. The dramatic decrease in Alaskan salmon abundance at ~100 BC is contemporaneous with warming of marine waters in the Santa Barbara basin, California[18,19]. Increased abundances of Alaskan salmon after ~AD 1200 correspond to a period of glacial advances in southern Alaska[20] and the Canadian Rockies[21], whereas high-resolution palaeoclimatological data from western North America show a dramatic shift at ~AD 800–1000 to drier conditions[22,23].

Twentieth-century monitoring of primary and secondary production and fish catch data also suggest that marine productivity along the west coast of North America is roughly divided by the Subarctic Current, which flows eastward to meet the coast near the Queen Charlotte Islands. Oscillating modes of productivity between the northern versus southern waters have been observed historically[3,24]. Our reconstruction of Alaskan salmon abundance is out of phase with the low-frequency long-term trends in both Pacific sardines (*Sardinops sagax*) and Northern anchovies (*Engraulis mordax*) over the past 1,700 years from the Santa Barbara basin[25] (Fig. 4). From ~AD 300 to AD 1200, sardines and anchovies were more abundant when Alaskan sockeye stocks were much weaker than average, whereas a reversal of this trend is apparent for the last ~800 years. The relatively high abundances of both sardines and anchovies[25], as well as proxies of upwelling and productivity from the Santa Barbara basin[19] and Gulf of California[26], indicate that the coastal zone off California was more productive from ~AD 300 to AD 1200. Patterns inferred from fish bones deposited in southern coastal British Columbian sediments indicate that fish productivity was also higher from ~0 to AD 1000 (ref. 27, Fig. 4). Thus the pattern of opposite trends in Alaskan salmon and the Pacific Northwest to California fish productivity was sustained for long periods, and was of greater amplitude than regimes in the twentieth century. The strong coherence of changes in regional fish populations and palaeoclimatic trends supports the hypothesis of linkages between ocean–atmosphere circulation and northern Pacific ecosystems, and suggests major changes in modes at ~BC 100 and AD 1000–1200.

The long-term trend reported here is distinct from the pattern seen in historical records, where sardines covary with salmon, but are out of phase with anchovies[5,6]. An additional pattern of variability not apparent in catch data, but revealed through our high-resolution palaeoecological analysis, is one in which sardines, anchovies and Alaskan salmon undergo synchronous in-phase fluctuations, such as those observed from the early 1800s through to the mid-1900s (Fig. 4). These relationships, revealed on different timescales, suggest that multiple modes of variability in ocean–atmosphere circulation and ecosystem dynamics operate in the northern Pacific. The unique low- and high-frequency relationships that we observe highlight the value of long records in identifying patterns in fish stock dynamics.

Contemporary monitoring and catch records have provided only a limited understanding of fish population dynamics and their responses to climatic change. However, palaeolimnological and palaeoceanographic investigations can greatly expand our knowledge, and provide an essential perspective on the magnitude and duration of fish stock variability. Our ~2,200-year reconstructions of Alaskan sockeye salmon abundances demonstrate that an unprecedented shift to a very low productivity regime, lasting centuries, can occur even without the influence of fisheries and other anthropogenic impacts. Synchronous variability between the few other palaeoceanographic records and our data strongly suggests that climate-related factors may greatly influence fish abundances over large geographic areas. A more thorough understanding of the linkages between climatic change and ocean ecosystems is critical for future sustainable management of northern Pacific fisheries, as fish stocks are now faced with many additional stresses including commercial fishing, habitat degradation and global warming. □

Methods

Undisturbed surface sediment cores were obtained from the lakes using a hand-operated gravity corer with a messenger-activated valve, specifically developed for collecting high-resolution surface cores. Age control for the past ~300 years is based on ^{210}Pb and ^{137}Cs dating and identification of volcanic ash layers[8]. Longer cores were obtained with a percussion corer, and the records were spliced together at a volcanic ash layer dated to ~AD 1710. Age control before this ash is based on accelerator mass spectrometry (AMS) radiocarbon dating of terrestrial macrofossils, and correlation of volcanic ash layers. A predominant ash found in all cores has been dated to 20 BC in the Frazer lake core. For Karluk lake, three additional AMS dates were obtained above this ash, and an age model was constructed using a third-order polynomial fit ($r^2 = 0.99$) with these four dated intervals and the two ash layers found in the surface cores (Katmai AD 1912, and the ~AD 1710 ash). The Akalura and Frazer lakes age models were constructed from regression equations ($r^2 > 0.95$) using the three ash dates. The character of the sediment cores is uniform throughout (except for the ashes), suggesting no hiatuses or anomalies (such as turbidites) in the depositional process.

Cores were sampled continuously at 0.5-cm intervals. Nitrogen isotopes were measured on dried, homogenized, bulk samples using a Finnigan Delta Plus mass spectrometer. Isotopic analyses are reported in standard δ notation relative to atmospheric N₂. Analytical precision is better than ±0.2‰. Isotope analysis of replicated cores collected from Karluk lake shows excellent reproducibility of the coring, isotope and dating techniques. Diatom slides were prepared following standard methods[28]. At least 400 valves were identified and enumerated along central transects of the coverslip for each sample, using a Leitz DMRB microscope equipped with differential interference contrast (numerical aperture, 1.30; magnification, 1000 ×).

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Sexual conflict reduces offspring fitness in zebra finches

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Parental care is often costly[1]; hence, in sexually reproducing species where both male and female parents rear their offspring (biparental care), sexual conflict over parental investment can arise[2]. Such conflict occurs because each care-giver would benefit from withholding parental investment for use with another partner, leading to a reduction in the amount of care given by one parent at the expense of the other[3–5]. Here we report experiments to explore the prediction from theory that parents rearing offspring alone may provide greater parental investment than when rearing offspring together with a partner[3,5]. We found that when the number of offspring per parent, and hence the potential workload, were kept constant, offspring received a greater per capita parental investment from single females than from both parents working together, and that males reared by single mothers were more sexually attractive as adults than their biparentally reared siblings. This difference between single- and two-parent families is due to a reduction in care provided by

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females when they care together with a male, rather than laziness by males or differences in the begging behaviour of chicks, supporting the claim that sexual conflict in biparental care can reduce the quality of offspring raised[3,5].

The importance of conflicts in evolutionary processes has been increasingly recognized in recent years[6–9]. In particular, sexual conflict over mating (pre-zygotic conflict) or parental investment (post-zygotic conflict) may be a powerful force shaping the potential for sexual selection[2,10], speciation[11] and the determination of life-history characteristics[12]. Although pre-zygotic sexual conflicts such as sperm competition are well characterized[13–17], there are very few demonstrations of the effects of post-zygotic sexual conflict on offspring fitness[18]. We used zebra finches (*Taeniopygia guttata*) to explore theoretical predictions from models of sexual conflict[3,5], which suggest that in some circumstances, single parents should provide greater parental investment per chick and at greater cost to themselves, compared with rearing chicks with a partner.

Fourteen pairs of zebra finches were allocated equally to one of two groups once clutches had hatched. Females in each group raised one brood of four chicks with the male, and one brood of two chicks alone, but the order in which this was done was different in the two groups. In group 1, the male was removed by replacing the cage partition and placing him in the half away from the nest and female (see Methods). Brood size was maintained at, or reduced to, two when the chicks were 4–5 days old, by which time chicks are able to self-thermoregulate. The female then reared these chicks alone until they reached independence at 35 days, when the young were removed to a separate cage. This was the 'uniparental care' regime. The male and female were then re-united by the removal of the cage partition, and were allowed to start a second clutch. Both parents then reared the brood, which was adjusted as necessary so that the pair raised twice as many offspring (four) as the female had reared on her own (two). This was the 'biparental care' regime. In group 2, the order was reversed so that the biparental care regime preceded the uniparental care regime.

Consequently, in both of the groups each female experienced both treatments (uniparental and biparental care) consecutively, so that any effects of variation in parental investment on offspring fitness were not confounded by genetic effects. However, unlike previous male-removal experiments[19–23], which have generally shown that a single mother is unable to provide enough food for the full brood, we also simultaneously reduced brood size so that the number of chicks per parent remained constant. As the shape of the curve relating chick fitness to parental investment is likely to be set by the number of chicks per parent, any differences in parental
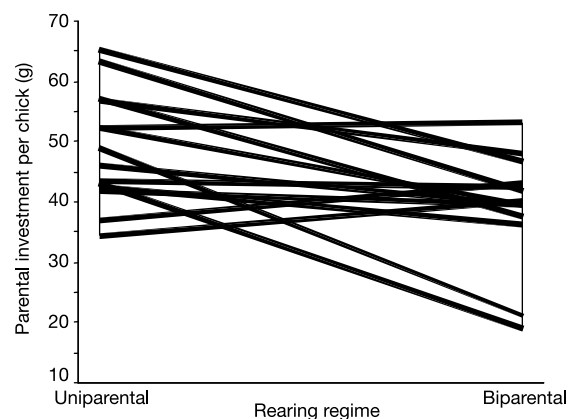

Figure 1 Parental investment for uniparental and biparental rearing regimes over a 15 day period after manipulation. Lines represent individual females. Our measure of parental investment, the amount of food consumed per chick, was greater under uniparental care (repeated measures general linear model, $F_{1,12} = 9.93$, $P = 0.008$).