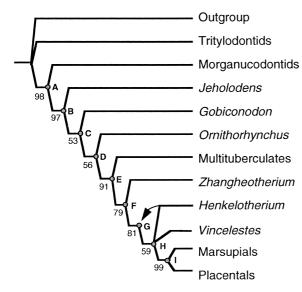**Figure 5** Evolutionary relationships of *J. jenkinsi*, gen. et sp. nov. The derived characters related to a mobile pectoral girdle occur separately on nodes B and E. The 'primitive' characters related to an immobile pectoral girdle occur in tritylodontids and the cynodont outgroup, and separately in *Ornithorhynchus* (node D). This indicates that there are many homoplasies of pectoral girdles and forelimbs (in contrast to the few or no convergences in the pelvic girdle and hindlimb), given the same tree topology of major clades of mammals. The arrow indicates an alternative placement of *Henkelotherium* at node G. For details of phylogenetic analysis see Methods and Supplementary Information.

characters, which allow a greater range of excursion of the shoulder joint in the locomotion of multituberculates[3,19,20] and living therians[21], have evolved at least twice among the Mesozoic mammals.

Alternatively, the mobile joints between the clavicle, interclavicle and scapula could be ancestral conditions shared by *J. jenkinsi* and the more derived mammals. If so, then the rigid clavicle–interclavicle articulation and relatively immobile scapula of monotremes (Fig. 3) would have to be regarded as atavistic reversals to the primitive conditions in the more distantly related non-mammalian cynodonts[16,22]. For either evolutionary scenario, we must conclude that the pectoral girdles and forelimbs of early mammals underwent extensive convergent evolution, not only by comparison with the dental and cranial features, but also in relation to more conservative features of the pelvis and hindlimbs. □

Methods

Phylogeny of mammals (Fig. 5) is based on a strict consensus of two equally parsimonious trees (tree length = 210; consistency index = 0.638; retention index = 0.724) from PAUP analysis (3.1.1. Branch and Bound search) of 101 dental, cranial and postcranial characters that can be scored for the 12 major clades of mammals (see Supplementary Information). Most of the characters are preserved in the holotype of *Jeholodens jenkinsi*. The two most pasimonious trees differ only in the alternative placements of *Henkelotherium*, which either is at node G (represented by an arrow in Fig. 5) or switches positions with *Vincelestes*. These alternative placements of *Henkelotherium* do not alter the positions of any other clades, including *J. jenkinsi*. Numbers on branches represent the percentage of bootstrap values in 1,000 bootstrap replicas for a 50% majority bootstrap consensus tree that has identical topology to one of the two most parsimonious trees (that in which *Henkelotherium* is positioned at node G).

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Strong effects of weak interactions in ecological communities

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The loss or removal of individual species can cause dramatic changes in communities[1–5]. Experiments indicate that in many communities only a few species will have such strong effects, whereas most will have weak effects owing to small *per capita* effects and/or low abundance[3,6–15,16]. But extinction of these 'weak' interactors could significantly alter natural communities because they play important stabilizing or 'noise-dampening' roles[14,15,17–23]. I

demonstrate here that some 'weak' interactors may also be important by magnifying spatiotemporal variation in community structure. An analysis of published interaction strength data shows that the greatest variation in species effect occurred for the weakest interactions. A field experiment corroborates this and shows how indirect interactions can generate an inverse relationship between the mean and variance of a consumer's impact on its prey. When a species' effects are highly variable in sign and magnitude, they may average to seem weak over broad scales but be strong in local contexts. Thus, what is frequently considered to be 'noise' in species interaction data may be a critical part of the signal.

Three recent empirical studies were among the first to quantify the distribution of per capita interaction strengths among a suite of consumer–prey interactions using a common metric[6–8] (see Methods). As in many empirical studies, species effects were identified as 'weak' when the removal or addition of a species failed to cause a statistically discernible mean change in the abundance of a target species. In each of these studies, a subset of the interactions that were considered 'weak' or zero on average were extremely variable among replicates (Fig. 1). For all three studies, the largest estimated range of interaction strengths among replicates occurred for species with mean effects that were considered 'weak' or 'insignificant'. In addition, the variation among replicates for these weak interactions was of the same order of magnitude as (or greater than) the strongest mean effects observed. These empirical patterns suggest two things: (1) before dismissing 'weak' interactors as unimportant, it may be important to distinguish between those with effects that are consistently weak versus those with strong, but variable, effects that average to be weak; and (2) by identifying 'strong' interactors solely by their mean impact, we may inadvertently be emphasizing those characterized by low variance. These possibilities question the basis of conservation strategies that attempt to prioritize research and management according to mean interaction strengths of species[24]. Therefore, it is critical to understand what mechanisms might generate high variability in the effects of weak interactors.

Weak effects of one species on another may be expected to be more variable than strong ones under some circumstances. The net effect of a species on a target species includes a suite of direct and indirect interaction pathways that often have effects of opposite sign. Thus a species may be empirically identified as weak if its direct and indirect effects on a target species counterbalance each other. If no single direct interaction dominates, indirect effects may create large variances in the net effect on the target species because of fluctuations in the abundance of other species mediating the strengths of indirect effects. By contrast, a disproportionately strong direct effect on the target species may swamp natural variation in indirect effects and result in a consistently strong net effect.

Using a simple rocky-intertidal food web as a model system, I experimentally tested the relationship among the strength of a consumer's mean direct effect on a prey, the importance of indirect effects, and the consistency of the net impact. In contrast to the studies reviewed above, I measured 'effect strength' as a consumer's collective impact (that is, per capita effect × density) on the abundance of a target species in order to quantify more directly the consequences of a species loss in a particular situation. Rather than compare effects of different consumers, my experiments held species identity constant and manipulated effect strength as a heuristic tool to compare variability of weak and strong effects. This approach avoided confounding factors of different species having different natural histories. Although it is simple to manipulate the density component of effect strength, altering the per capita effect is less straightforward. One proposed approach for weakening the per capita effect of a predator on a target species is to add alternative prey, assuming that the predator must then trade off some of its preference for consuming the target species[17]. In this study, I manipulated both consumer density and the presence of an alternative prey species. However, adding the alternative prey species also added potentially important and confounding indirect effects on the target species. Therefore, I focus on the results of altering predator density as a tool for manipulating its collective effect strength on the target species and for examining the influence of indirect effects on the outcome of predation.

The study was conducted on the rocky, central coast of Oregon, USA, in mid-intertidal disturbance patches that consisted primarily of predatory whelks and two groups of sessile prey, mussels and acorn barnacles[25]. The mid-intertidal zone was dominated by a bed of the large California mussel, *Mytilus californianus*, which is characterized by a mosaic of disturbance patches. In the first year of succession, the patch food web consisted primarily of predatory snails (whelks: *Nucella emarginata* and *N. canaliculata*) and two species of its early colonizing sessile prey (mussels: *Mytilus trossulus*; and acorn barnacles: *Balanus glandula*). Although whelks have a negative direct effect on mussels, potential indirect effects of whelks on mussels mediated through barnacles can be both positive and negative depending on the recruitment intensity of barnacles. Barnacles directly facilitate the recruitment of mussels[25], so whelks can have a negative indirect effect on mussels by eating barnacles. However, at high barnacle densities, some thinning of barnacles by whelk predation can strengthen the remaining barnacles' attachment to the rock, thereby having a positive indirect effect on mussels by increasing the stability of their settlement substrate. Therefore,
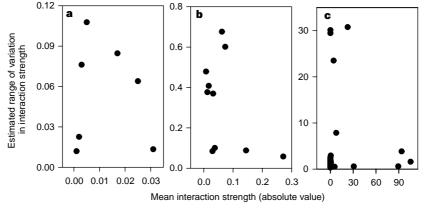

Figure 1 Estimated range of variation in interaction strength versus the mean strength for three studies that quantified *per capita* interaction strengths among a suite of consumer–prey interactions. **a**, Effects of six rocky intertidal grazers on kelp[6]; **b**, effects of preying mantids on arthropod prey[7] (three cases were omitted where the denominator of the interaction strength index was ≤0 when estimating its variation); and **c**, effects of six estuarine predators on six benthic invertebrate prey in the Ythan river estuary, Scotland[8].

this 'simple' interaction web is ideal for testing whether and/or when indirect interactions are important in generating high variation in the effects of a consumer on its prey. When the direct effect of whelk predation on mussels is weak, its net impact should be more variable than if the direct effect is strong, because a weak direct effect would be more sensitive to variation in the strength of indirect effects mediated through barnacles.

To test this hypothesis, I conducted two experiments. The first quantified how the strength of the direct, pairwise effect of whelks on mussels varied with whelk density. In this 'mussel transplant' experiment mussels were transplanted to otherwise
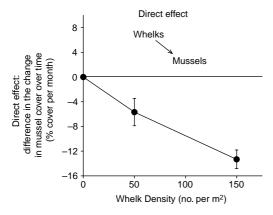
Figure 2 Mean (±s.e.) direct, pairwise effect of whelks on mussels that were transplanted to achieve constant initial cover, for each of the three densities of whelks enclosed. One-way blocked ANOVA on the change in mussel cover over time: whelk effect significant, $P = 0.01$, d.f. = 2, MS = 120.4, $F = 13.0$. Linear regression of the change in mussel cover over time for the three whelk densities: $R^2 = 0.71$, $P = 0.001$.

bare plots so that all had similar initial mussel cover, and whelk density was manipulated using enclosures (see Methods). Whelks had a significant negative direct effect on mussel cover. The strength of this direct effect increased linearly with whelk density (Fig. 2) such that the per capita effects of whelks remained constant across the density of whelks manipulated. All else being equal, the density treatments successfully altered the strength of the direct, 'collective', or 'population-level' effect of whelks on mussels. Based on the results of this transplant experiment, I considered the direct, population-level effect of low- versus high-density predation on mussels to be analogous to 'weak' versus 'strong' predation, respectively, when other factors (such as the presence/absence of alternate prey) were equal.

A second 'factorial experiment' manipulated all combinations of predator density (none, low and high) and the presence of alternative prey (barnacles) (see Methods). With this design, I quantified the degree to which the net impacts of weak and strong predation on mussels were differentially sensitive to indirect effects mediated by barnacles. All treatments were replicated in each of four separate disturbance patches in the mussel bed, and the entire experiment was repeated (in separate plots in the same four patches) over three successive starting dates (1991, 1992 and 1993) which varied naturally in the recruitment of barnacles (Fig. 3 inset). This design allows the consistency of whelk impacts on mussels to be assessed in the face of spatial or temporal variation in barnacle abundance.

When barnacles were removed, both low- and high-density predation had similarly consistent negative direct effects on mussels (Fig. 3a–c). These results differ from those of the transplant experiment (Fig. 2) because mussel colonization is naturally low when barnacles are not present to facilitate recruitment[25]. Thus, with no alternative prey, both predator treatments essentially eliminated the few mussels that settled[25]. Note also that the whelks' direct effect (Fig. 3a–c) is consistently smaller in magnitude
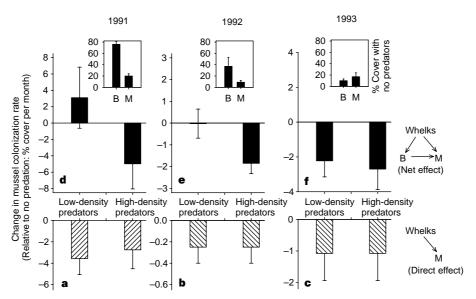
Figure 3 Mean (±s.e., $n = 4$) effect of low- and high-density predator treatments on mussel colonization (relative to predator exclusions) for each of the three experimental starting dates. **a–c**, Newly settled barnacles were removed monthly, and thus the effects of predation include primarily direct effects on mussels (M) alone. **d–f**, Barnacles (B) were allowed to colonize, and thus the effects of predation included both direct effects and indirect effects mediated by barnacles. The effect of predator density varied with the presence of barnacles and this interaction varied among starting dates: predator density × barnacles × start date was significant: $P = 0.0001$, $F = 6.44$, d.f. = 6. The effects of low- and high-density predators did not differ significantly from each other in any of the barnacle-removal treatments (F-protected least-squares means: $P > 0.6$ in all

cases). Where barnacles were present, low- and high-density predator treatments differed significantly in 1991 and 1992, but not in 1993 (F-protected least-squares means: $P = 0.008$, 0.037 and 0.287, respectively). Insets: Variation among years in the cumulative recruitment and mortality of barnacles and mussels in the absence of predation and interspecific competition. Data are mean (±s.e.) covers of barnacles (B = *B. glandula*) and mussels (M = *M. Trossulus*) averaged over time for each year. Barnacle colonization varied significantly among years: ANOVA on barnacle cover in insets, effect of year: $P = 0.010$, $F = 12.79$, d.f. = 2. Mussel colonization did not vary significantly between years: ANOVA on mussel cover in insets, effect of year: $P = 0.42$, $F = 1.01$, d.f. = 2.

than the net effect of that whelk treatment (Fig. 3d–f). This is due to the fact that, even if whelks completely eliminated mussels in the absence of barnacles, because fewer mussels settle when barnacles are absent (compared to when they are present), the difference in mussel cover between treatments with and without predators is necessarily small.

When barnacles were present, low- and high-density treatments had qualitatively different net effects on mussel colonization. Strong (that is, high-density) predation was insensitive to the presence of barnacles and continued to have negative net effects on mussel colonization for all three starting dates (Fig. 3d–f). However, the mean net effect of weak predation varied in sign between starting dates and was directly related to annual variation in barnacle abundance (Fig. 3d–f). It ranged from weakly positive in 1991 to zero in 1992 to negative in 1993. Averaged over all three starting dates, the net effect of weak predation was close to zero (a change of 0.28% mussel cover per month) and thus statistically not significant. However, the range of variation among years in the mean net effect of weak predation was greater in magnitude than the largest mean net effect observed under strong predation (Fig. 3d–f: mean net effect of weak predation ranges from +3.1 in 1991 to −2.2 in 1993 versus mean net effect of strong predation of −5.0 in 1991).

In treatments where indirect effects due to barnacles were present, weak predation magnified variation in mussel colonization rates relative to no predation, whereas strong predation had a dampening effect (Fig. 4). This pattern was consistent both among replicates within a given experimental starting date as well as among starting dates (Fig. 4). The only case when weak predation reduced variation in mussel colonization relative to no predation was in 1993 when barnacle recruitment was low and their associated indirect effects unimportant (Figs 4 and 3c, f and inset).

Therefore, in this simple intertidal interaction web, when the direct effect of predation was weak, the net effect varied more in sign and magnitude than when predation was strong. All else being equal, the mean net effect of weak predation on mussels was more sensitive than strong predation to indirect effects mediated by barnacles. This resulted in greater variability in mussel colonization, both spatially among replicates and temporally among experimental starting dates, for weak predation than either no or strong predation. More important, the standard deviation of the weak predation effects equalled or exceeded the mean effect size of strong predation. Thus, although the net effect of 'weak' predation was not statistically significant on average,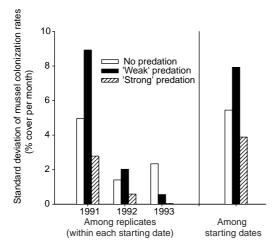 it was ecologically important in generating variation among replicate patches and among years in mussel colonization rates.

Because the mid-intertidal mussel bed is characterized by a mosaic of disturbance patches, a species' impact that varies greatly among patches may cause divergence of early successional trajectories, and thus increase among-patch heterogeneity in community structure[25]. For example, in the present study individual replicate plots with barnacles under weak predation diverged rapidly in species composition. Eight months after the 1991 experimental disturbance, these weak predation replicates ranged from domination by barnacles (72% *B. glandula*; 17% *M. Trossulus*) to domination by mussels (28% *B. glandula*; 68% *M. Trossulus*). This pattern is consistent with other observations that this system is typified by disturbance patches of the same age differing dramatically in species composition[25,26].

More generally, these and other results[15,17,21] challenge the assumption that research and management should focus solely on species that exhibit strong mean impacts on community structure (such as keystone species[14,24]). In doing so, they broaden our understanding of the consequences of species loss for community organization. First, the total effect of deleting a species includes both density and per capita effects, and the effect of a species when rare can be qualitatively different from that of the same species when abundant[27,28]. Second, although species effects that are consistently weak may have important stabilizing effects on communities[17], a subset of species effects that are weak on average may be characterized by high variance. The latter can be due to a greater influence of indirect interactions when the direct effect is weak. Conditions that can generate high variation in the effect of a consumer on a target prey include when direct and indirect effects are opposite in sign, and when the balance of direct versus indirect effects shifts easily with variation in the abundance of alternative prey. Because indirect interactions are widespread in natural communities, 'weak' (but strongly variable) interactors may play an important, but unappreciated, role in maintaining landscape-scale diversity if their effects on species abundances are strongly context-dependent, or highly variable over space and time. A critical challenge for ecologists is thus to evaluate more generally the conditions under which weak interactions magnify rather than dampen variation in natural communities, and to understand the consequences of variable species impacts for community and ecosystem organization. □

Methods

Analysis of published interaction strength data. These three studies[6–8] were chosen for analysis because they used a common metric and were the only ones of this type where estimates of variation in the interaction strength index can be obtained from the published data. All three studies measured per capita interaction strength using an index proposed by Paine[6], which is expressed as: $(E - C)/(C \times P)$, where E and C are prey abundance in treatments where predators are present and absent, respectively, and P is predator density. Although per capita effects are not the same as the total impact of deleting a species, I chose to use the metric that was originally used when they distinguished between strong and weak interactors. Paine[6] provided bootstrapped estimates of standard error (s.e.) and the number of replicates for each grazer–algae interaction strength measured. In this case, a potential range of variation for each interaction was estimated as the experimentally determined mean interaction strength ± 1 s.d. Fagan and Hurd[7] provided s.e. for prey abundance in each treatment (C and E), but not for the interaction strength index. In this case, a range of variation was estimated by recalculating the index using ($C + 1$ s.d. and $E - 1$ s.d.) and ($C - 1$ s.d. and $E + 1$ s.d.). Raffaelli and Hall[8] provided 95% confidence intervals for prey abundance in the C and E treatments. In this case, a range of variation was estimated as for Fagan and Hurd's study, but with confidence intervals instead of s.d.

Mussel transplant experiment. Small mussels (<2.5 cm shell length) were transplanted to 20×20 cm plots that were scraped of macroscopic organisms (see ref. 23 for transplanting technique). Mean initial cover of mussels in all plots was $57 \pm 2\%$, and the change in mussel cover was monitored after 6

Figure 4 Variation in mussel colonization rates (per cent cover per month) between individual replicates ($n = 4$ disturbance patches) within each separate experimental starting date and between means of each starting date. Data are standard deviations of colonization rates for each predator density in treatments where barnacles were allowed to colonize.

months, when mussel cover in some replicates approached zero. In each plot, whelk densities were manipulated using 20 cm × 20 cm stainless steel cages attached to the rock. Cages either excluded whelks or enclosed two or six whelks corresponding to a range of densities naturally observed (0, 50 and 150 whelks per m², respectively). All treatments were replicated in four large patches in the mid-intertidal mussel bed. One high-density replicate was lost because of winter storm damage. Whelk effects were quantified as the difference in mussel colonization rates (change in per cent cover per month) between −whelk treatments and +whelk treatments (either low or high density). Although the results and conclusions were qualitatively identical when effects were measured using Pain's[6] index (data not shown), I present effect strengths in terms of the difference in colonization rates because this measure, unlike Pain's, does not assume equilibrium prey abundance[16,29].

Factorial experiment. All plots were initially scraped bare and both mussels and barnacles colonized naturally. Whelks were enclosed at three different densities (0, 50 and 150 whelks per m²) in 20 cm × 20 cm cages, and for each whelk density, barnacles were removed monthly from half the cages. All treatments were initiated in April over three successive years: 1991, 1992 and 1993. The interactive effects of predator density (none, low, high), barnacles (present, absent) and start date (1991, 1992, 1993) on mussel colonization rate was analysed using a randomized block ANOVA. Repeated measures was not used because, although all three experimental runs were initiated over 3 years in the same blocks, individual plot localities differed between years. Data (per cent cover per month) were arcsine (square root)-transformed for analysis.

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Anticipation of moving stimuli by the retina

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A flash of light evokes neural activity in the brain with a delay of 30–100 milliseconds[1], much of which is due to the slow process of visual transduction in photoreceptors[2,3]. A moving object can cover a considerable distance in this time, and should therefore be seen noticeably behind its actual location. As this conflicts with everyday experience, it has been suggested that the visual cortex uses the delayed visual data from the eye to extrapolate the trajectory of a moving object, so that it is perceived at its actual location[4–7]. Here we report that such anticipation of moving stimuli begins in the retina. A moving bar elicits a moving wave of spiking activity in the population of retinal ganglion cells. Rather than lagging behind the visual image, the population activity travels near the leading edge of the moving bar. This response is observed over a wide range of speeds and apparently compensates for the visual response latency. We show how this anticipation follows from known mechanisms of retinal processing.

Because a moving object often follows a smooth trajectory, one can extrapolate from its past position and velocity to obtain an estimate of its current location. Recent experiments on motion perception[5–7] indicate that the human brain possesses just such a mechanism: Subjects were shown a moving bar sweeping at constant velocity; a second bar was flashed briefly in alignment with the moving bar. When asked what they perceived at the time of the flash, observers reliably reported seeing the flashed bar trailing behind the moving bar. This flash lag effect has been confirmed repeatedly[8–10], and various high-level processes have been invoked to explain it, such as a time delay due to the shift of visual attention. To assess whether processing in the retina contributes to this effect we analysed the 'neural image' of these two stimuli at the retinal output. We recorded simultaneously the spike trains of many ganglion cells in the isolated retina of tiger salamander or rabbit. The responses to flashed and moving bars were then analysed by plotting the firing rate in the retinal ganglion-cell population as a function of space and time.

Figure 1 illustrates the responses of individual OFF-type ganglion cells to a dark bar flashed briefly over the receptive-field centre. In both salamander (Fig. 1a) and rabbit (Fig. 1b), the cells remained silent for a latency of ~50 ms, then fired a burst of spikes that lasted another 50 ms. When the bar was swept over the retina at constant speed (Fig. 1c, d), these same cells fired for a more extended period, beginning some time before the bar reached the position at which the flash occurred, and extending for a shorter time thereafter. When the bar was swept in the opposite direction (Fig. 1e, f), it produced a very similar response, showing that these cells had no direction-selective preference.

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