Linkages between stream and forest food webs: Shigeru Nakano's legacy for ecology in Japan

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During the 1990s, ecologists such as Gary Polis catalysed a renaissance in food-web research by focusing on trophic processes occurring among habitats at the landscape scale. Examples include prey transported across ecotones to subsidize predators in adjacent habitats, which, in turn, can have strong indirect effects such as initiating trophic cascades. Recent work in Japan by Shigeru Nakano and his colleagues has set new standards of holism and rigor in food-web research by demonstrating complementary seasonal shifts in prey fluxes across a stream–forest ecotone that sustain higher densities and diversities of consumers in both habitats than would otherwise be supported in either alone. Although Nakano died in a tragic accident at sea with Polis and three other Japanese and American ecologists in March 2000, his work has left an indelible legacy that gives direction and purpose to further research on the significance of complex interrelationships in food webs across landscape scales.

Published online: 17 July 2002

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Food webs, describing the links among consumers and their prey in ecological communities, have a long history of study in ecology dating back to Charles Elton's research in the 1920s [1,2]. Subsequently, however, experimental work on food webs has focused within habitats on the effects of species interactions (e.g. competition and predation) and physical factors (e.g. disturbance) on community composition and dynamics through time [3]. By contrast, food-web theory largely addressed architectural features of published food webs (connectance, species richness and food-chain length) that influenced system stability in models [4–7]. In the 1990s, a renaissance occurred in research on food webs as better empirical data describing highly resolved food webs emerged from a variety of systems [8,9]. In particular, as ecologists began viewing the world more broadly, they began to consider trophic processes occurring across habitats at the landscape scale, rather than focusing primarily on food-web links within habitats. For example, Gary Polis became intrigued by the role of marine-derived allochthonous organic matter (i.e. sea wrack washed up on beaches) in supporting unusually high densities of spiders on desert islands off the coast of Baja California [10]. Subsequent work showed that these predators caused a trophic cascade, suppressing terrestrial herbivorous insects and thereby indirectly defending island plants [11]. This led Polis *et al.* [12] to champion the view that food webs are often 'subsidized' by the movement of materials, energy or organisms across habitat boundaries from adjacent ecosystems. They reasoned that such resource subsidies might strongly affect recipient communities, for example by maintaining high densities of predators that initiate trophic cascades.

Recently published research on stream ecosystems by Shigeru Nakano and his colleagues in Japan, who had followed Polis' work closely, built on these ideas and has made major advances at the frontiers of food-web ecology. During the past five years, other ecologists began demonstrating the importance of spatial dynamics of prey movements across the aquatic–terrestrial interface [13–16], but Nakano and his colleagues also became interested in how these fluxes varied through time. Their most recent study demonstrated that reciprocal complementary seasonal shifts in fluxes of prey between a stream and its forested watershed sustained higher densities of consumers in both habitats than would otherwise be supported in either habitat alone [17]. This research broke new conceptual ground, exploring temporal shifts in fluxes and food-web controls across landscape scales, and presenting some of the best data ever amassed on the dynamics and community impacts of cross-habitat subsidies [3].

Tragically, both Gary Polis and Shigeru Nakano, along with another American and two Japanese ecologists, died when their boat capsized in a violent storm in the Sea of Cortez while returning from one of Polis' island study sites [18–20]. Although Nakano started from relatively humble academic beginnings in Japan, he had risen rapidly to reach a pinnacle in both Japanese and international ecology, which was demonstrated by the interest that world leaders in food-web research such as Polis took in his work. Here, we show the origins of Nakano's research on spatial and temporal subsidies that link stream and terrestrial food webs, summarize the most recent findings, place them in context with other studies, and consider his legacy for future research in this field.

Ecology in Japan, and the origins of Nakano's research

Appreciating the unique nature of Shigeru Nakano's work requires understanding some of the history of ecology in Japan. Scientific inquiry in Asia emanated from China to Japan and emphasized holistic views of organisms and ecosystems, including an early description of biological control in a food web with

  PII: S0169-5347(02)02572-7

three trophic levels that predated Elton by more than 1600 years [21]. The reductionism of Western science, including the scientific method and the central role of experiments, came to Japan only after the Meiji Restoration in 1868 when European philosophies entered the country again after the ban on trade during the Edo Period was lifted. By 1950, Japanese ecologists had made important contributions to population ecology and bioenergetics [22], and had developed a theory of habitat segregation based on aquatic insects in streams [23–27]. An important figure was Kinji Imanishi, a professor at Kyoto University, who catalysed inquiry by young Japanese ecologists into the importance of individuality in the social structure of animals, including primates and fishes [28–29], the pivotal role of dispersal in population ecology [30], and density-dependent habitat selection [31], as well as several aspects of plant population and community ecology [32] (see also [21]). Working from this foundation, Japanese ecologists developed theories that predated Western ideas on individual-based approaches to population ecology (*cf.* [33]), the role of dispersal in metapopulation ecology, and Fretwell and Lucas' [34] ideal-free distribution theory [21]. Poor conditions for conducting large-scale experiments and field studies in Japan prompted other Japanese ecologists to pursue theoretical ecology, where major advances were also made [35–41]. These significant contributions to ecology are even more impressive given that there are far fewer ecologists in Japan than in the USA or Europe. Moreover, until recently, there were very few food-web or stream community ecologists [33], so little research was conducted in these areas in Japan before 1990.

The holism that characterizes Japanese science, the tradition of detailed observational studies on fishes, and previous work in Japan on the role of individuality and dispersal in the population ecology of fishes (reviewed in [33]), strongly influenced Nakano's approach to stream ecology. Nakano brought to his research a deep love and rich understanding of the details of the natural history of mountain streams in central Japan and their biota, which he developed during boyhood angling and snorkeling. He began research on native landlocked masu salmon *Oncorhynchus masou* in Japanese mountain streams as an undergraduate, continuing on in graduate school to conduct individual-based studies of movement and growth [42,43]. He also worked on the behavioral ecology of cichlids in Lake Tanganyika [44]. His doctoral research included highly detailed studies of dominance hierarchies in stream salmonids, which are among the most complete works ever done in this field [45–47]. One of these papers [46] is cited in a recent ecology textbook as among the best examples of interspecific dominance hierarchies [48]. Nakano's innovative insights and approaches to field ecology led to an international collaboration on research into behavioral mechanisms promoting coexistence in coevolved salmonid guilds in mountain streams of Hokkaido Island in northern Japan and in Montana [49–52] (*cf.* [18]).

Controls on biodiversity in forest-stream food webs

In 1995, Shigeru Nakano accepted a new position as Assistant Professor at the Tomakomai Experimental Forest of Hokkaido University, and a few years later was promoted to Associate Professor and Director. Here, he began to ask new questions about the factors that promote biodiversity in both streams and their riparian forests. Although it was well known that streams are strongly influenced by organic matter subsidies from their terrestrial watersheds in the form of allochthonous leaf and litter input [53], Nakano pondered a different question. How important, he wondered, are streams to biodiversity in the riparian forests that they traverse, and how strong are the food-web linkages between the two habitats? His search for answers was strongly influenced by Polis' papers on spatial subsidies across ecotones like the forest–stream interface [10,11]. The ensuing research required Nakano to develop strong collaborations with ecologists who understood the terrestrial biota, such as forest birds and spiders, as well as he himself understood the stream biota. He assembled and led a team of graduate students and postdoctoral researchers in a coordinated set of observational and experimental field studies of these terrestrial and aquatic food webs, and redirected a group of forestry technicians to build the apparatus required for one of the largest-scale field manipulations conducted to date in streams. These studies could not have been achieved without the unique combination of an excellent field site, a well-developed infrastructure for ecological research and the substantial technical support that Nakano assembled at the Tomakomai Experimental Forest.

Since 1995, Nakano and his colleagues have published four major papers on the interrelationships of terrestrial and aquatic food webs, several of which have set a new standard for food-web research. Their study site, Horonai Stream, is a spring stream that is fed by an aquifer of volcanic tuff and traverses a hardwood forest of oak *Quercus crispula* and ash *Fraxinus mandshurica*. The riparian zone is inhabited by an assemblage of insectivorous birds, including residents, such as the great tit *Parus major*, and migrants, such as the narcissus flycatcher *Ficedula narcissina* and winter wren *Troglodytes troglodytes*. The stream supports a guild of insectivorous salmonids, including native masu salmon, Dolly Varden charr *Salvelinus malma* and whitespotted charr *S. leucomaenis*, but has also been invaded by the non-native rainbow trout *O. mykiss*, which make up about half or more of the total fish biomass in many reaches. Although stream ecologists had long known about the role of allochthonous detritus from forests (i.e. dead leaves and litter) in supplying organic matter to stream macroinvertebrates (*cf.* [54]), only recently has the importance been recognized of direct inputs of terrestrial invertebrates that provide high-quality prey that subsidize stream fishes (e.g. [55]). Recent research has shown that the biomass of terrestrial prey inputs into headwater forested streams can equal the *in situ* production of bottom-dwelling (benthic) macroinvertebrates [56]. In the first paper by Nakano's group [57], an observational study comparing this prey flux from forested versus grassland reaches into Horonai Stream, Kawaguchi and Nakano reported that fish adjusted their abundance to match the input of terrestrial prey. They showed that the biomass of the entire guild of salmonids, including rainbow trout, was twice as high in forested reaches than in adjacent grassland reaches in most seasons, and that inputs of terrestrial prey in the forested reaches were also nearly double those in adjacent grassland reaches. Terrestrial prey were crucially important to fish bioenergetics, making up half of the total annual prey consumption by salmonids. These results suggested that this prey resource subsidy plays an important role in regulating fish biomass through 'bottom-up' control.

In a second paper, Nakano *et al.* [58] also demonstrated the strong influence of this terrestrial prey subsidy in mediating the 'top-down' effects of fish on benthic macroinvertebrates and attached algae (periphyton) during the summer. They excluded terrestrial prey from replicate 50-metre stream reaches using greenhouse canopies (Fig. 1), and also manipulated the presence of the native Dolly Varden charr, which are adept at foraging directly on benthic invertebrates when drifting aquatic prey are scarce [50,52]. When denied access to terrestrial prey inputs, which contributed more than half their annual energy budget in control sections, Dolly Varden preyed heavily on herbivorous benthic insects, thereby releasing periphyton from grazing and causing increased algal biomass – an archetypal 'top-down' trophic cascade [59]. By contrast, control sections without fish, canopy, or both had high densities of herbivores and low algal biomass. Thus, although terrestrial invertebrates contributed a much smaller biomass flux from forest to stream compared with detrital inputs, this summer subsidy of terrestrial prey clearly had strong indirect effects on the stream community.

An even more striking finding in a third paper was that aquatic invertebrates emerging from the stream provide important prey subsidies to terrestrial consumers during seasons other than summer [17]. Nakano and Murakami measured fluxes of terrestrial prey falling into the stream and aquatic prey emerging into the forest monthly for 14 months, and determined the contribution of these allochthonous prey to the entire assemblage of resident and migrant birds (ten species) and stream fishes (four salmonids and the strictly benthivorous sculpin *Cottus nozawae*). They made >13 000 observations of avian foraging,

Fig. 1. Horonai Stream, the main study site for Shigeru Nakano's food-web research team. A portion of the stream canopy used by Nakano *et al.* [58] to exclude terrestrial prey across the forest-stream ecotone is shown (photo by Shigeru Nakano).

of which prey could be identified as aquatic or terrestrial for >7000, and examined >1400 fish stomach samples by nonlethal pumping. They found that the cross-habitat flux of aquatic prey from the stream to forest contributed 50–90% of the monthly energy budget during fall through spring for four winter-resident bird species, and made up 98% of the diet of a fifth species, the winter wren. Overall, including the summer leaf-out period when birds foraged primarily on terrestrial invertebrates, aquatic prey made up 26% of the total annual energy budget of the entire forest bird assemblage. In turn, during the summer leaf-out period, terrestrial prey input made up 60–100% of fish diets, and 44% of their total annual energy budget overall. This study set a new standard for holism and rigor in food-web ecology by quantitatively addressing questions relevant to landscape scales, but with close attention to the phenology, diet and behavior of the species mediating these cross-habitat interactions [3].

A fourth recent study [60] suggests that the invading rainbow trout also have strong effects that could cascade through these aquatic–terrestrial food linkages and potentially affect forest birds. Nakano *et al.* showed that rainbow trout actively selected terrestrial prey over aquatic prey, because of the larger size of terrestrial prey and their peak flux into streams during the evening versus the smaller size of drifting aquatic macroinvertebrates and the nocturnal emergence of adult aquatic insects. They reported that rainbow trout consumed 77% of the total dry mass input of terrestrial prey into a reach during mid-summer, and that this constituted 73% of their daily ration. If fully consumed, terrestrial prey represented sufficient energy to support the entire rainbow trout population in the reach during the summer. These results suggest that if the riparian habitat were modified in ways that reduced the input of terrestrial prey, rainbow trout would be forced to forage more intensively on aquatic drifting prey, or directly on the benthos. Moreover, when drifting prey are scarce, native Dolly Varden charr shift foraging modes to feed directly on the benthos [50,52]. In either case, there is a potential for strong effects on aquatic macroinvertebrates, their emergence and, ultimately, the flux of aquatic prey that subsidizes forest birds. Ongoing research is aimed at elucidating the strength of these potentially surprising cross-habitat linkages in this same ecosystem.

Nakano's role in defining new frontiers for studies of food webs

Three dimensions, space, time and energy flow, define real food webs, yet community ecologists have, in the past, focused on only one or two of these at a time. Nakano's contribution of the idea of seasonal controls on trophic exchange among habitats is one of the first major conceptual advances to unite these three dimensions in a framework that is sufficiently simple and elegant to be tested empirically in nature. The idea immediately suggests exciting cross-continental comparisons in ecosystems with different patterns of seasonal productivity fluctuations in coupled habitats [3]. Nakano and several of his former students visited the Eel River on the north coast of California, which flows through a forested watershed under a Mediterranean climate regime. River-to-forest insect fluxes and their importance to spiders, lizards and bats have been studied at this site [16,61–63], providing a starting basis for collaborative comparisons of habitat exchange under Mediterranean versus western Pacific climate regimes.

Ecologists attempting to project the consequences of changes in global climate regimes for ecosystems have predicted dislocations, such as the re-alignment of seasonal phenologies of flowers and pollinators, or predators and prey [64,65] (reviewed in [66]). Nakano and one of his graduate students obtained, to our knowledge, the first experimental results demonstrating a thermally mediated change in trophic cascades in a flume study showing recoupling of Dolly Varden, insect grazers and algae under different temperatures (D. Kishi and S. Nakano, unpublished). Such experiments should be performed in other systems and extended to the field, where thermal regimes are being rapidly altered not only by atmospheric changes, but also by local and regional land use, including water extraction and deforestation.

In 1999, Nakano accepted a position at the Center for Ecological Research at Kyoto University, where he was also planning collaborations with Masahiko Higashi to address the dynamic links between detrital and producer-based chains in food webs, a fundamental area also of central interest to Polis and his colleagues [67]. Higashi, one of the most accomplished theoretical ecologists in Japan in the 1990s (e.g. [37,40–41]), was drowned in the same accident that claimed the lives of Nakano and Polis. Higashi *et al.* [68] developed a theoretical framework that allows empiricists to account for complex partitioning of energy or elemental constituents in food chains with omnivory. Although developed before the widespread use by ecologists of stable isotopes as food-web tracers, this framework should prove to be invaluable for tracking elements through food chains in ways that allow us to sort out the spatial sources and scales of food web interactions (e.g. [16,69]). The broad vision, imagination, clarity and energy of these two Japanese scientists will be sorely missed as future ecologists grapple with these important problems.

Looking toward the future

The tragic accident in Baja California took the lives of three of Japan's best ecologists, Shigeru Nakano, Masahiko Higashi [70,71] and Takuya Abe [71,72], who studied the ecology of termite societies in tropical forests. The tragedy was especially difficult for Nakano's family, friends and colleagues, because his body was never recovered [18]. It was also a great loss for the fields of stream ecology and food-web ecology, because his innovative approaches promised to yield many more exciting discoveries that would have revolutionized these fields. In the aftermath of the accident, his colleagues have picked up the pieces and are moving forward. Many of the threads of his work will be continued by his collaborators and graduate students, and many remaining data sets are now being published (e.g. [73–80]). It is clear that, in spite of his tragic loss at a young age, Shigeru Nakano has left an indelible legacy that gives direction and purpose to the work of many young researchers in Japan and throughout the world, where his innovative research on the important interconnections between forest and stream food-webs is now being read and recognized.

Acknowledgements
We thank M. Inoue, Y Taniguchi, and four anonymous reviewers for constructive comments that helped improve this review. Research and travel by K.D.F. in Japan has been generously supported by the National Science Foundation since 1991 (INT 9016512, INT 9602574, DEB 0108222), and by two Senior Research Fellowships from the Japanese Society for the Promotion of Science in 1994 and 2001. M.E.P. thanks the National Science Foundation (DEB 961517) and the California Water Resources Center (UCAL-WRC-W-906) for their support. M.M. received generous support from the Japanese Ministry of Education, Science, Sport, and Culture (Nos. 09NP1501, 11440224).

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Begging for control: when are offspring solicitation behaviours honest?

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There is burgeoning interest in the idea that conspicuous begging displays, when parents are provisioning dependent young, advertise offspring need honestly to parents. Many empirical studies claim to support the theory of honest signalling of need, where parents control resource allocation. The evidence, however, also fits the predictions of recent models for the evolution of costly begging where offspring control allocation. These models incorporate variation in offspring condition and show that the three main predictions of honest signalling models are also found with models of sibling scramble competition. Consequently, it is difficult to discriminate between the two different modelling approaches from their predictions, despite their having been the focus of much empirical work. In particular, the evidence indicates that the prediction that begging intensity signals offspring need honestly is strongly context dependent. Begging might be 'honest' only when the potential for conflict is low and food is not limiting.

Published online: 11 July 2002

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Ever since Trivers [1] showed that parents and their offspring could be in conflict over the amount of parental investment, the evolution and maintenance of begging behaviour has been an area of increasing interest to evolutionary biologists. Trivers considered the relationship from the point of view of the offspring, and saw begging as a form of psychological manipulation by the offspring to obtain a higher amount of parental investment than the parents were selected ideally to give. Subsequent theoretical treatments of begging have tended to model the allocation of parental provisioning to dependent young in terms either of the outcome of scramble competition among siblings (i.e. offspring control parental investment allocation [2–5]), or, more recently, in terms of honest signals [6] of offspring 'need' (i.e. parents control parental investment allocation [7,8]). So, are family dynamics regarding provisioning controlled primarily by parents or by their offspring?

Since Kilner and Johnstone [9] reviewed the evidence for honest signalling, more recent work has cast some doubt on the stability of the honest-signalling solution [10,11] (but see [12]). Nevertheless, increasing numbers of recent empirical studies claim to support honest signalling [13–16]. Here, we re-evaluate critically the application of honest signalling to the evolution of costly begging displays in the light of recent models of sibling scramble competition [17,18], which show that the primary predictions generated by honest-signalling models and scramble models are not mutually exclusive (Box 1).

Key predictions of honest-signalling theory

When delivering food to dependent young, parents often face a barrage of extravagant begging calls and postures. If the brood size is greater than one, the parent has to make a decision as to which of its young to feed and, if the current load is divisible, how much to feed each offspring. Information received by parents during feeding bouts might also influence future feeding episodes and affect overall provisioning rate [12]. Consequently, the decision-making processes surrounding the feeding of dependent young by parents are a dynamic, and potentially complex, series of interactions.

Models of offspring solicitation are based on key simplifying assumptions (Box 1). Kilner and Johnstone [9] reviewed the evidence for begging as an honest signal of need based on three main predictions of honest-signalling models: (1) begging intensity should reflect offspring need, (2) parents should provision young in relation to begging intensity and (3) begging should be costly. However, as Kilner and Johnstone acknowledge, neither prediction 2 nor 3 is unique to honest signalling. In both scramble and honest-signalling models, an offspring that begs more receives more food, and both models require a cost of begging. Kilner and Johnstone found little firm support for predictions 2 and 3 – possibly owing to the simplicity of these predictions in relation to the complexity of the behaviour – but they concluded that the empirical data provided good support for the first prediction, which is

  PII: S0169-5347(02)02565-X