

Interspecific social dominance networks reveal mechanisms promoting coexistence in sympatric charr in Hokkaido, Japan

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Abstract

1. Coexistence of species requires equalizing mechanisms that minimize fitness differences, which are balanced by stabilizing mechanisms that enhance negative intraspecific interactions versus interspecific ones. Here, we develop a simple theoretical framework that allows measuring the relative strength of intraspecific versus interspecific competition in dominance hierarchies. We use it to evaluate mechanisms promoting coexistence between two congeneric charr that compete for foraging positions, which strongly influence density-dependent growth and survival.
2. Agonistic interactions ($n = 761$) among 71 Dolly Varden *Salvelinus malma* and whitespotted charr *Salvelinus leucomaenis* were measured by snorkelling in two pools in the sympatric zone of a Hokkaido stream during two summers. Interspecific dominance hierarchies, analysed using three methods, were closely correlated with fish length but the species treated each other equally. Ranks for the most dominant fish in each pool, determined directly by knockout experiments, were also virtually identical to ranks by length.
3. Similarly, exponential random graph modelling of the social networks provided no evidence that either species was dominant over the other. Instead, larger fish were more likely to win contests, especially over fish of the next lower ranks.
4. These results demonstrated that the two species were nearly ecological equivalents in accessing key resources in this sympatric zone. Nearly identical growth and stable densities over 4 years further supported this inference, although Dolly Varden were a minority (29% of the assemblage), a sign of some fitness difference.
5. Detailed foraging observations coupled with two concurrent studies revealed an effective stabilizing mechanism. Dolly Varden shifted to feeding directly from the benthos when drifting invertebrates declined, a behaviour enhanced by morphological character displacement, thereby partitioning food resources and enhancing intraspecific competition while avoiding agonistic encounters with whitespotted charr.
6. The plurality of evidence indicates that fitness differences between these ecologically equivalent species are small in this local assemblage, and balanced by

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resource partitioning, a modest stabilizing mechanism that promotes coexistence. The theoretical framework presented here is a useful tool to evaluate the strength of interspecific versus intraspecific competition, which combined with information on trade-offs in ecological performance can contribute to a mechanistic understanding of species coexistence.

KEYWORDS

Dolly Varden charr, ecologically equivalent species, interspecific competition, interspecific dominance hierarchies, mechanisms of stable coexistence, *Salvelinus*, social network analysis, whitespotted charr

1 | INTRODUCTION

The mechanisms by which species coexist in communities have been of persistent interest to ecologists, particularly for species that appear very similar (Ellner et al., 2019; MacArthur, 1958). Ecological theory holds that stable coexistence between two species requires that each species has a greater effect on its own per capita population growth rate than it does on its competitor, or fundamentally that intraspecific competition is greater than interspecific for each species (Adler et al., 2018; Siepielski & McPeck, 2010). However, in real landscapes coexistence often occurs through mechanisms that operate at different spatial scales (Chesson, 2000). Equalizing mechanisms, such as differences in survival across space owing to environmental factors such as temperature, can reduce fitness of a competitively superior species in locations where an inferior species is favoured by the environment, thereby equalizing fitness. In turn, at the scale of these local assemblages, coexistence can occur when stabilizing mechanisms such as resource partitioning are sufficient to balance the remaining fitness differences among species (Adler et al., 2007).

Most theories and tests of coexistence have been based on population models describing exploitative competition among plants (Hart et al., 2018; see McPeck & Siepielski, 2019) or animals with little or no size structure or complex behaviour, such as zooplankton (Gliwicz & Wrzosek, 2008; Tilman, 1981). In contrast, mechanisms promoting coexistence among animals with more complex behaviours that compete for resources by interference have been studied relatively little (Grether et al., 2013, 2017; Morse, 1974). This is a serious information gap because a wide variety of mammals (Sushma & Singh, 2006), birds (López-Segoviano et al., 2018), reptiles (Langkilde & Shine, 2004), fish (Nakano, 1995a) and invertebrates (Turra & Denadai, 2004; Yitbarek & Philpott, 2019) compete within interspecific dominance hierarchies for territories or other resources, such as vacant shells among hermit crabs. Interspecific behavioural interference likely evolved from exploitative competition for defendable resources, resulting in convergence or persistence of displays recognized by both species (Grether et al., 2017). This interspecific aggression can set range limits and constrain abundance (Jankowski et al., 2010; Pasch et al., 2013), and result in temporal or spatial habitat partitioning in

sympatry, leading to stable coexistence at local to landscape scales (Grether et al., 2013).

The outcome of interference competition between species is often asymmetric (Culbertson & Herrmann, 2019; Martin et al., 2017) and usually based on adult body size (Langkilde & Shine, 2004; Wilson, 1975). Many animals that compete by interference also display indeterminate growth with no fixed adult size, and form size-structured populations, such as fish (Nakano, 1994, 1995b) and hermit crabs (Rotjan et al., 2010). In these cases, both species and size may be important in determining dominance, and hence access to resources.

The effect of interspecific competition and its role in coexistence of species depends on interactions among individuals, and the consequences these interactions have for demographic rates such as growth, survival, and reproduction (McPeck & Siepielski, 2019; Peterson et al., 2004). In most cases, interference competition among individuals is studied in the laboratory, or in field enclosures, with juveniles or adults of the same size. However, such experiments can introduce artefacts owing to lack of population size structure, artificially high densities, and artificial conditions such as unnatural food delivery or lack of natural physical habitat. This provides an incomplete understanding of the mechanisms of coexistence, because competition among individuals actually plays out in size-structured dominance hierarchies, and in natural habitats where the species are syntopic.

Here, we develop a simple theoretical framework that allows measuring the relative strength of intraspecific versus interspecific competition in a size-structured dominance hierarchy of two species. We employ this framework in a field study of free-ranging organisms, two congeneric charr (*Salvelinus*; Salmonidae) that compete for foraging positions in size-structured dominance hierarchies within stream pools in a zone of sympatry. The results allow evaluating hypotheses about the balance between fitness differences and stabilizing mechanisms that promote coexistence in this local assemblage. Moreover, when combined with findings from a set of field comparative studies and field and laboratory experiments on the zoogeography, ecology, evolution and behaviour of these species, the findings provide a plurality of evidence for mechanisms that explain how and why these species coexist across a hierarchy of local to landscape scales (Siepielski & McPeck, 2010).

2 | MATERIALS AND METHODS

2.1 | Theoretical framework

Dominance hierarchies are common among many animal taxa, and can determine access to territories or other spatially defined resources, food, and mates which, in turn, have profound effects on growth, survival, and reproduction (Chase & Seitz, 2011). The relative importance of size and species in determining ranks of individuals in interspecific dominance hierarchies leads to a simple theoretical framework for testing the strength of intraspecific versus interspecific competition in a two-species assemblage (Figure 1). For example, if the species are each arranged in size-structured populations, and compete for positions in an interspecific dominance hierarchy, then their relative dominance rankings can be used to distinguish among four alternatives:

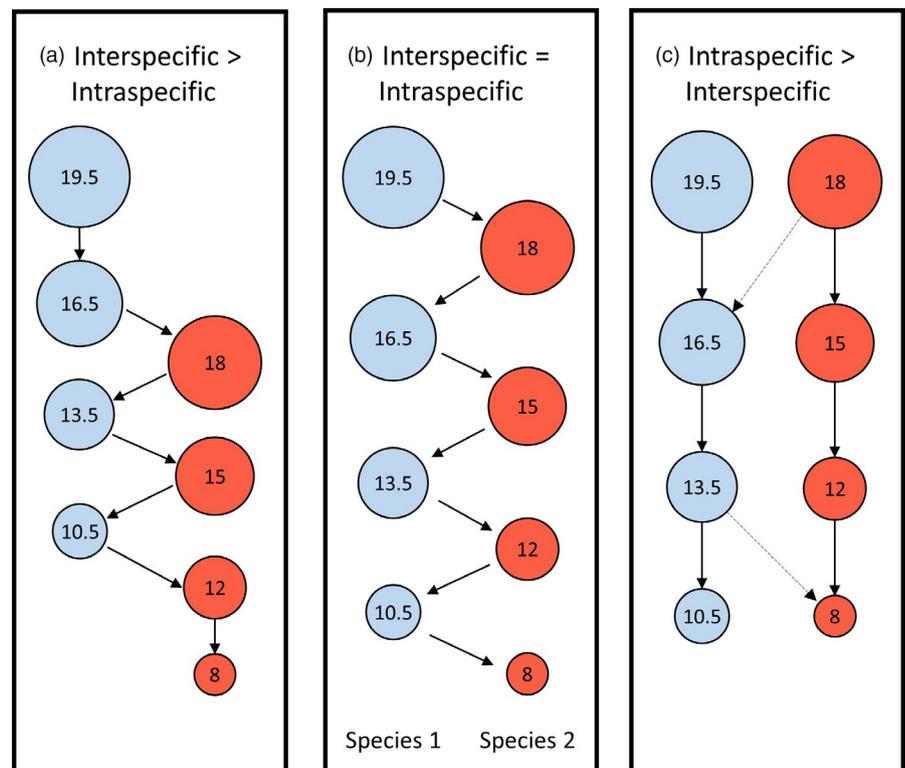
1. Interspecific competition \gg intraspecific (not shown in Figure 1)—Dominance is based on species alone, so that even the smallest individual of the dominant species is able to dominate the largest individual of the subordinate species.
2. Interspecific competition $>$ intraspecific (Figure 1a)—Dominance is based on species and size, so that smaller individuals of the dominant species are superior competitors than larger individuals of the subordinate species and gain access to more or better resources.
3. Interspecific competition = intraspecific (Figure 1b)—Dominance is based on size alone, so larger individuals are dominant and gain access to resources, regardless of species.

4. Intraspecific competition $>$ interspecific (Figure 1c)—Species use largely different resources (e.g. by resource partitioning) and interact behaviourally much less with heterospecifics than conspecifics, so dominance hierarchies are largely intraspecific.

2.2 | Study system

Two species of charr native to Hokkaido Island, northern Japan, provide an ideal study system for employing this theoretical framework to test the relative strengths of competition in the field. Evidence from mitochondrial DNA indicates that Dolly Varden charr *Salvelinus malma* colonized the island during the Pleistocene from an adjacent region (Yamamoto et al., 2014), followed later by its congener, the whitespotted charr *Salvelinus leucomaenis* (Yamamoto et al., 2004). Dolly Varden now occur in upstream reaches throughout the island and whitespotted charr downstream, with relatively narrow zones of sympatry defined by temperature (Fausch et al., 1994). This zone of overlap increases in elevation along a climate gradient, from the northeast where mean annual air temperature is 5°C and Dolly Varden occur alone, towards the southwest where temperature averages 8–9°C and only whitespotted charr occur except in one cold spring. Across the island, transition points between sympatry and Dolly Varden in allopatry (or each species in parapatry) occur at a consistent threshold of mean air temperature during the growing season (10–12°C during April to October; see figure 4 in Fausch et al., 1994).

FIGURE 1 A simple theoretical framework for testing relative strength of intraspecific versus interspecific competition in two-species dominance hierarchies. See text for explanation of the three cases. Coloured circles indicate two species, and numbers refer to individual lengths. Arrows show one-sided dominance interactions between dominant and subordinate individuals. Dashed arrows are weak interactions



Laboratory experiments showed the importance of water temperature to the outcome of interspecific competition. At age 0, whitespotted charr dominated Dolly Varden by aggressive interference, held more favourable upstream positions, foraged more, and grew and survived better at 12°C than 6°C in a laboratory stream (Taniguchi & Nakano, 2000). In contrast, at 6°C Dolly Varden were about equal competitors, grew similarly, and survived much better than whitespotted charr. These results were confirmed in a replicated field experiment on growth of age-0 charr in cold versus warm tributaries (mean: 7.4 vs. 11.8°C; Watz et al., 2019), and provide a mechanism to explain their longitudinal distribution in Hokkaido streams.

In sympatric zones, both species occupy pools and compete in interspecific dominance hierarchies for positions from which they make forays to capture drifting invertebrates (Nakano & Furukawa-Tanaka, 1994). Positions near the heads of pools, and downstream from velocity refuges, provide the most net energy for stream salmonids (Fausch, 1984) and are vigorously contested (Nakano, 1995a, 1995b). Fausch et al. (1994) also reported density compensation across individual pools in a sympatric zone, an indirect measure of interspecific competition (Wiens, 1989). Moreover, as the shared resource of drifting invertebrates declined throughout summer, Dolly Varden shifted from sit-and-wait foraging to ranging widely around pools and picking benthic invertebrates from the streambed (Nakano & Furukawa-Tanaka, 1994), a behaviour facilitated by their subterminal jaw morphology. A replicated field experiment coupled with a comparative field study over four summers confirmed that declines in drifting prey were the mechanism causing the foraging mode shift (Fausch et al., 1997; Nakano et al., 1999), and that it occurred at a specific prey encounter rate. Further research revealed character displacement among Dolly Varden towards shorter heads and more subterminal jaws in sympatry versus allopatry, and individuals with these characteristics had more benthic prey in their diets (Nakano et al., 2020).

2.3 | Alternative hypotheses

Here we measure the interspecific dominance hierarchies of Dolly Varden and whitespotted charr in pools of a natural stream in Hokkaido, to test two plausible alternative hypotheses for mechanisms promoting coexistence in this simple assemblage. Given the ability of whitespotted charr to dominate in laboratory and field experiments, one alternative is that interspecific competition by this species against Dolly Varden is greater than intraspecific (alternative 2 in the theoretical framework above; Figure 1a), so that whitespotted charr dominate Dolly Varden of larger size. For example, Nakano (1995a) found that individual masu salmon *Oncorhynchus masou* were dominant over whitespotted charr up to about 15% greater in body length, owing to such differences in competitive ability. In this case, we predict that relatively strong stabilizing mechanisms such as spatial storage effects or divergent phenotypes are required to

balance the large difference in fitness and achieve species coexistence (Adler et al., 2007; Chesson, 2000).

In contrast, a second alternative is that the competitive abilities of these congeneric charr are similar and based primarily on size. In this case interspecific and intraspecific competition are nearly equal (alternative 3; Figure 1b) and we predict that only modest stabilizing mechanisms such as partitioning resources during periods of scarcity are required to promote coexistence in sympatry.

2.4 | Study area

The study was conducted in the sympatric zone of Poroshiri Stream, a third-order mountain stream in south-central Hokkaido (see Appendix S1 for further details). Stream morphology is primarily step pools created by boulders with cobble-gravel substrate. Mean water temperature in the study reach during the June–July 1991 and 1992 study periods was nearly identical (8.6 and 8.7°C).

Density of whitespotted charr was 2.4 times that of Dolly Varden ($M \pm SD$: $0.34 \pm 0.03/m^2$ vs. $0.14 \pm 0.01/m^2$) and stable across 4 years (1991–1994; Nakano et al., 1999). Length-at-age of the two species was also nearly identical across the four summers. Fork lengths of age-1 through age-4 fish averaged 10.7, 13.8, 16.2, and 18.4 cm ($n = 146$ whitespotted charr, $n = 121$ Dolly Varden).

The charr interspecific dominance hierarchies were measured in two pools about 100 m apart in the 2.0-km sympatric segment, one near the downstream terminus of a major tributary (Pool A) and the other in the main stream (Pool B). Both were nearly rectangular (A: 4×5 m; B: 5×7 m) and had maximum depths of 70 cm.

2.5 | Measuring dominance hierarchies

Interspecific dominance hierarchies were measured by underwater observation from one or two fixed locations near the downstream ends of pools (see Appendix S1 for details, Figure S1). A grid of coloured rocks placed at 1-m intervals provided spatial references. Visibility averaged about 4 m, and all fish were visible from diver positions. Fish positions and behaviour were recorded on transparent plastic graph paper overlaid on scale maps of pools (Figure S2). Focal points (positions, hereafter) of all charr 8 cm or larger (age-1 and older) were recorded during scan observations (Altmann, 1974) made at about 30–60 min intervals (Figure S3). Most fish were individually identifiable by species, length, unique marks and location of positions. Fork lengths (FL) of fish were estimated (nearest 0.5 cm) by comparing fish to streambed features later measured. Regressions of estimated versus actual lengths of fish later captured ($r^2 = 0.94$, $n = 22$) and the length–mass relationship ($r^2 = 0.99$, $n = 20$) were used to predict length and mass for fish not measured.

Foraging and agonistic behaviour of individual fish were recorded during 5-min focal-animal observations (Altmann, 1974; Figure S4). Agonistic behaviour of fish initiating encounters was classified as charge, chase, nip, frontal display, lateral display or

approach, and that of receiving fish as flee, lateral display, avoid or ignore (after Kalleberg, 1958; Noakes, 1980). Dominance matrices were constructed from the results of one-sided attacks, where the receiving fish fled (Nakano, 1995b). Cases where the receiving fish, or both fish, exhibited lateral display were considered draws. Those where attacks were avoided or ignored were excluded. Foraging attempts were classified as benthic, midwater or surface (Nakano & Furukawa-Tanaka, 1994).

Dominance hierarchies were mapped during five 4–16-day periods from late June to mid-July of 1991 and 1992 (Table S1). Two periods were defined for Pool B in 1991 because many fish had left or redistributed during a 2.5-day hiatus. We also conducted 12 'knock-out' experiments (Pinter-Wollman et al., 2014) during four of five periods. For these, the most dominant individual in each pool was removed by angling while observing it underwater by snorkelling (Figure S5) and changes in positions of the remaining fish recorded. A total of one to four of these dominant fish were sequentially removed from each pool, and dominance hierarchies were mapped for medians of 19.5 scans before any removals and 14 scans after each removal.

2.6 | Data analysis

We used three methods to estimate dominance hierarchies and their characteristics, and exponential random graph models (ERGM), a tool from social network analysis, to test relationships of dominance with species and body length (see Appendix S1 for details). We also used knockout experiments to determine dominance directly for the top-ranking 3 to 5 fish in each pool.

2.6.1 | Estimating dominance hierarchies

We selected three methods for estimating dominance hierarchies recommended by Sánchez-Tójar et al. (2018) to achieve robust inferences: the I&SI method (Inconsistencies & Strength of Inconsistencies; de Vries, 1998), David's score (David, 1987), and the randomized Elo rating method (Neumann et al., 2011). We calculated the I&SI and David's score using the R package (R version 3.6.1; R Development Core Team, 2019) and ELO-RATING v. 0.46.11 (Neumann & Kulik, 2014), and the randomized Elo rating using the R package ANIDOM v. 0.1.4 (Farine & Sánchez-Tójar, 2017).

We evaluated the uncertainty in dominance hierarchies estimated from the randomized Elo rating method based on (a) repeatability of 1,000 randomized ratings and (b) rank correlation of hierarchies calculated from split datasets (Sánchez-Tójar et al., 2018). We also assessed the uncertainty in dominance rankings among the three methods using Spearman's rank correlation.

McDonald and Shizuka (2013) reported most dominance hierarchies ($n = 40$ published datasets) were transitive (i.e. linear), ranks were stable through time, and David's scores or Elo ratings that determined rank dropped steeply. Using EloRating, we calculated

the index of triangle transitivity (Shizuka & McDonald, 2012), an index of the stability of rank order (Neumann & Kulik, 2014), and steepness based on David's scores (de Vries et al., 2006), and evaluated the significance of transitivity and steepness using randomization tests. We compared dominance rankings, triangle transitivity, steepness, and stability with and without draws to assess their influence.

2.6.2 | Social network analysis

Exponential random graph models (ERGM) are a powerful tool within social network analysis for identifying characteristics of individuals that explain the relationships among them (Harris, 2014; Pinter-Wollman et al., 2014). They have been used to evaluate factors influencing dominance hierarchies in animal social groups, including fishes and birds (Dey & Quinn, 2014; Dey et al., 2013, 2015). ERGMs are particularly useful when coupled with measures of dominance hierarchies because they can test for effects of phenotypic traits like species and body size on network structure (Silk & Fisher, 2017).

The ERGM use stochastic modelling to estimate the probability that a given pattern of interactions among network members is explained by a set of predictor variables, such as species and size (see Appendix S1 for details). We developed models to test three key predictions about factors influencing the contests won in these charr dominance hierarchies, based on the matrix of binary directed links. The R package ERGM v. 3.10.4 in *statnet* (Handcock et al., 2008) was used to fit the ERGM, using the structural term *edges* and three categorical or continuous node-based covariates (Silk & Fisher, 2017).

1. Larger fish were more likely to initiate and win contests than smaller fish—*nodecov (length)*
2. Fish were more likely to initiate and win contests against fish of similar size than ones of much different size—*absdiff (length)*
3. Fish were more likely to interact with members of their own species than the other species, termed species homophily—*nodematch (species)*

We evaluated model fit using Akaike's information criterion (AIC), and significance of covariates based on approximate Wald test statistics generated from Markov Chain Monte Carlo (MCMC) simulations. Goodness-of-fit was assessed by comparing a set of network properties of simulated networks to the observed network, including goodness-of-fit for in-degree, out-degree, edgewise shared partners and minimum geodesic distance, as well as for the model statistics (Luke, 2015; Silk & Fisher, 2017).

Spearman's rank correlation was also used to test the relationship between body length and dominance rank for each of the three methods used to estimate dominance hierarchies. This provided another direct method to assess how closely dominance hierarchies were related to length.

2.6.3 | Knockout experiments

Successive removals of fish holding the dominant position (hereafter alpha fish) allow determining the dominance hierarchy directly, because each successive subordinate fish is expected to move into the position vacated. We also assessed whether, after removing alpha fish, the next fish in the hierarchy selected similar positions when they became the alpha and beta fish. We plotted positions of successive alpha and beta fish in each pool for visual comparison, and also compared Euclidean distances between all pairs of alpha fish, beta fish and alpha-beta pairs of fish to assess the mean and SD within versus between groups.

3 | RESULTS

The three senior authors observed fish for 165 hr over 40 observation days in the two pools (Pool A 19 days; Pool B 21 days; Table S1). On average, fish were observed in each pool for 4.1 hr per day, or about 40% of the 10.5-hr observation period (07:30 to 18:00 hr). Periods of continuous observation by divers ($M \pm SD$: 2.1 ± 1.0 hr) were distributed nearly equally between morning (53%) and afternoon (47%). These observations yielded totals of 289 scans (range: 21–97 per pool-year combination) and 668 5-min focal-animal observations (range: 50–248) for 71 fish. We recorded a total of 761 one-sided dominance interactions (range: 75–219 per pool-year combination) and 36 draws (range: 0–14) making up 4.5% of all interactions.

3.1 | Dominance hierarchies

Charr dominance hierarchies estimated using three methods were highly orderly (i.e. linear), consisting of transitive triads with steep differences between ranks and ranks that were highly stable through time. All five hierarchies estimated for the two pools in the 2 years were perfectly transitive, based on the index of triangle transitivity ($t_{tri} = 1.0$; Table 1), although in two cases this was different than expected by chance only at $p = 0.09$. Steepness was highly significant for all hierarchies ($p = 0.001$) indicating that David's scores used to rank fish for this method differed sharply. The median stability index was 0.94 (range: 0.82–0.95) indicating that the dominance ranks were highly stable through time. Dominance ranks based on randomized Elo ratings largely predicted the outcomes of contests between charr, another indicator of steep hierarchies. The probability that the higher-ranking fish won was typically >0.90 for all five hierarchies, even when differences in rank were only 1 or 2 (Figure 2; Figure S6).

The uncertainty of the dominance rankings was low. Repeatability of Elo ratings based on 1,000 randomized networks was high (median: 0.97; range 0.96–0.99) and rank correlations among 1,000 randomized Elo ratings for split datasets were also high (median: 0.84; range 0.75–0.85). Both metrics are greater than the highest values

TABLE 1 Characteristics of interspecific dominance hierarchies among Dolly Varden and whitespotted charr in two pools in Poroshiri Stream during two summers. The 2.5% and 97.5% quantiles of Elo-rating uncertainty for split datasets are shown in parentheses

Pool	Period	Interactions per individual	Hierarchy			Elo-rating uncertainty		Rank correlation with length		
			Triangle transitivity	Steepness	Stability	Repeatability	By splitting	I&SI	David's score	Randomized Elo rating
A	1991	18.3	1.0 $p = 0.000$	$p = 0.001$	0.94	0.97	0.84 (0.67–0.96)	0.70 $p = 0.01$	0.91 $p < 0.0001$	0.85 $p = 0.0005$
	1992	17.7	1.0 $p = 0.09$	$p = 0.001$	0.95	0.99	0.80 (0.60–0.97)	0.98 $p < 0.0001$	0.89 $p = 0.002$	0.89 $p = 0.002$
B	1991 (early)	5.4	1.0 $p = 0.09$	$p = 0.001$	0.89	0.96	0.75 (0.52–0.91)	0.63 $p = 0.01$	0.64 $p = 0.01$	0.75 $p = 0.002$
	1991 (late)	6.9	1.0 $p = 0.002$	$p = 0.001$	0.82	0.97	0.84 (0.70–0.94)	0.78 $p = 0.0002$	0.71 $p = 0.001$	0.78 $p = 0.0002$
	1992	10.1	1.0 $p = 0.002$	$p = 0.001$	0.94	0.97	0.85 (0.72–0.94)	0.74 $p = 0.0003$	0.75 $p = 0.0002$	0.81 $p < 0.0001$

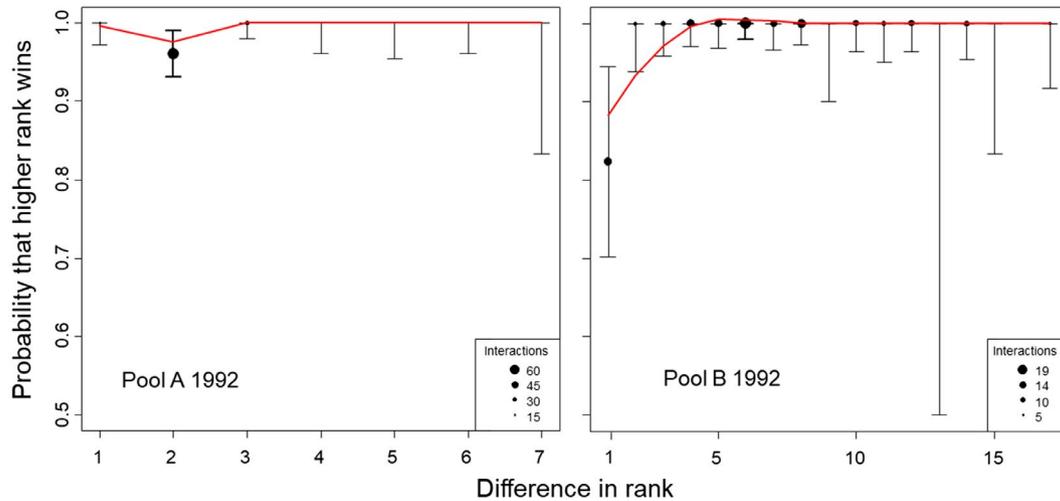


FIGURE 2 Hierarchy shape, indicated by the probability of the higher ranked charr winning as a function of difference in rank, for each pool in 1992 (plot generated using aniDom). Symbol size denotes number of interactions (see legend) and error bars are the 2.5% and 97.5% quantiles

for the steepest hierarchies simulated by Sánchez-Tójar et al. (2018), which were estimated with the most certainty. Three of five datasets had means of 10–20 interactions per individual (range: 5.4–18.3), as recommended by these authors, and they report that very steep hierarchies like these can be estimated with confidence at values even as low as 5.

Dominance rankings estimated by all three methods were closely aligned, and also closely correlated with ranks of fish by body length. Rank correlations among any pair of the three methods were high for all five hierarchies (median $r_s = 0.95$, range: 0.85–1.00, $n = 15$, $p < 0.001$ for all), so the average of all three was used as the final dominance ranking (Figure 3; Figures S7 and S8; Table S2). Dominance ranks estimated by each method were also highly correlated with ranks based on body length, and highly significant (median $r_s = 0.78$, range: 0.63–0.98, $n = 15$, $p \leq 0.01$ for all; Table 1). All measures of transitivity, steepness, stability, and uncertainty, and correlations among methods or with length were identical or nearly so when draws were included (K. D. Fausch, unpubl. results), so we report only those calculated after excluding the small proportion of draws.

3.2 | Importance of size versus species in dominance hierarchies

The ERGM supported the hypothesis that dominance hierarchies were organized by fish body length alone, and provided no evidence that either species interacted more or less with the other than expected. In each hierarchy, body length was a significant covariate accounting for links (*nodcov (length)*: $p < 0.0001$ for all; Table 2) and the positive coefficient indicates that larger fish were more likely to win contests than smaller ones. In four of five cases the absolute difference in body length was also significant or nearly so (*absdiff (length)*: $p = 0.0005$ – 0.06), and the negative coefficient indicates that fish

were more likely to interact with others of similar length than fish of quite different lengths. Hence, larger, more dominant fish were most likely to attack and win contests against fish of slightly smaller size, which occupied the next lower ranks. In the fifth case the simpler model without this non-significant ($p = 0.96$) covariate had a lower AIC value, but the results for all other covariates were identical in direction and significance so the more complex model is reported to facilitate comparison among hierarchies.

There was no evidence from four cases that contests were more or less likely between charr of the same species (i.e. homophily; *nodematch (species)*: $p = 0.10$ – 0.72). The signs of the significant covariates for homophily in Pool B in 1992 indicate that whitespotted charr were more likely to attack and win contests against conspecifics ($p = 0.002$) but Dolly Varden were less likely to win them against other Dolly Varden ($p = 0.008$). However, this was not unexpected because whitespotted charr were 2.5 times more prevalent in scans than Dolly Varden (mean number observed: 9.4 vs. 3.8) so the more abundant targets for whitespotted charr were conspecifics and for Dolly Varden were heterospecifics. The MCMC simulations for all models converged rapidly, and most of the 36–49 tests of goodness-of-fit of network characteristics were not significant indicating little lack of fit of the simulated networks compared to the observed one (Luke, 2015).

3.3 | Direct evidence from knockout experiments

When the most dominant (alpha) charr in each pool was removed, their position was filled by the next most dominant (beta) charr, usually within about 30 min. In three cases, the three or four knockout experiments showed that successively more subordinate charr in the hierarchy also quickly occupied the beta position when vacated (Figure 4; Figures S9–S11). In the fourth case, Pool A in 1992, the beta fish moved to the alpha position when the dominant was

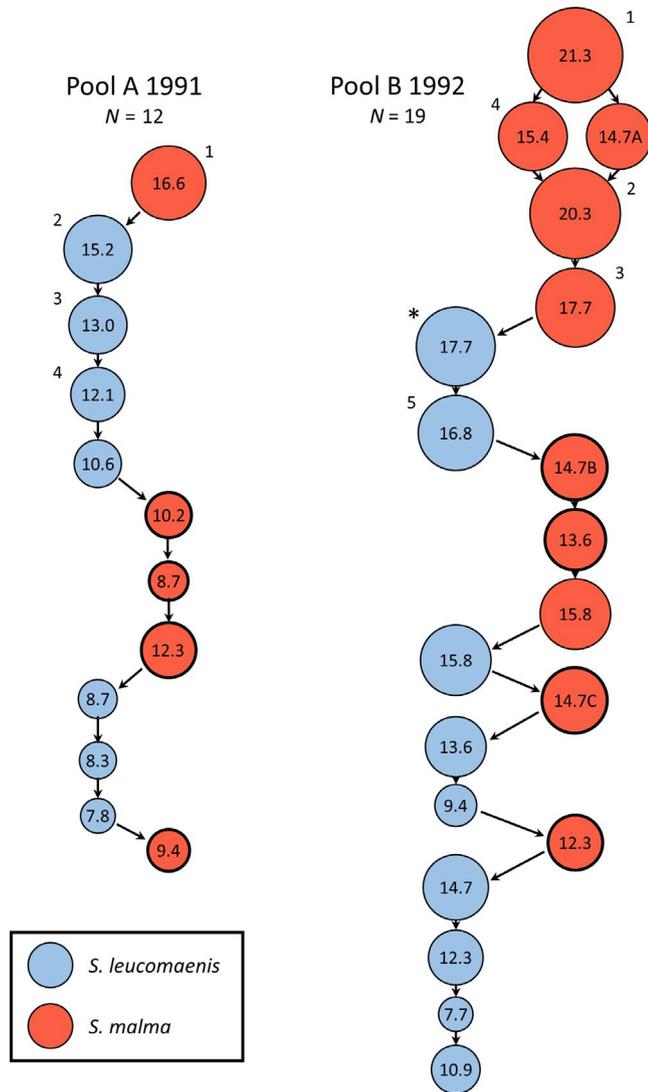


FIGURE 3 Mean charr interspecific dominance hierarchies for two representative pool-year combinations. Circles show fork length (cm), and arrows show mean dominance order based on three methods (see text). Numbers alongside top-ranking fish are dominance ranks determined directly by knockout experiments. Circles with bold outlines represent fish that frequently shifted to benthic foraging. The asterisk indicates one non-interactive fish

removed, but was later supplanted by another immigrant charr of similar length as the original alpha fish and quickly moved back to its original beta position (Figure S9).

The dominance order determined by this direct method matched the order by length exactly for the three to five most dominant fish that interacted in the hierarchy, with one exception, and was not related to fish species (Figure 3; Figures S7 and S8). In Pool B in 1992, a 15.4-cm Dolly Varden (originally ranked 4th in the hierarchy) was dominant over a 16.8-cm whitespotted charr, next in the hierarchy. In two other cases single large whitespotted charr (17.2 and 17.7 cm) held positions peripheral to the alpha and beta positions in Pool B and rarely interacted with other fish in the hierarchy (Figures S10 and S11).

There was no indication from knockout experiments that whitespotted charr were inherently dominant over Dolly Varden. In four of five hierarchies the largest one or two fish were Dolly Varden (Figure 3; Figures S7 and S8), and in two of these the knockout experiments revealed that large Dolly Varden were dominant even over whitespotted charr of equal or greater length. In the fifth case the two largest fish were whitespotted charr followed by a Dolly Varden, and the dominance ranks determined by knockout experiments matched their ranks by length.

The positions used by successive alpha fish were similar in each of the four sets of knockout experiments, and those of beta fish were also similar in the two conducted in Pool A (Figure 4; Figures S9–S11). Mean pairwise distances between centroids of alpha positions among periods ranged only 38 to 76 cm across the four sets (Table 3), and those between centroids of beta positions in Pool A were only 23 and 54 cm. In contrast, mean pairwise distances between alpha versus beta positions ranged 97 to 198 cm. In Pool B in both years, there were apparently more positions of similar quality for beta fish, some near alpha positions and some farther away. Mean pairwise distances were 117 and 145 cm, similar to mean distances between the alpha and beta positions.

3.4 | Foraging shifts

Dolly Varden are adept at switching foraging modes from drift to benthic feeding, and this was recorded frequently for specific charr in each pool (Figure 3; Figures S7 and S8). Fifteen Dolly Varden (1–4 per pool) of middle or lower dominance rank frequently shifted to benthic feeding (Table S2), and made a median of 66% of their forays to the benthos (range: 27%–96%). One small whitespotted charr, among the most subordinate fish in Pool B in 1991 (late period), also made more than half its forays to the benthos. In contrast, 50 other charr of both species made primarily midwater forays and only a median of 2.5% of forays to the benthos (range: 0%–17%; no foraging observations were made for five subordinate whitespotted charr). Eighty per cent (12 of 15) of Dolly Varden that switched engaged in little agonistic activity (i.e. won 0 or 1 bout against rivals), and when attacked during benthic foraging simply avoided the other charr.

4 | DISCUSSION

The simple theoretical framework developed here, and our test of its predictions using empirical data on the behavioural ecology of free-ranging animals, provide a unique opportunity to understand the mechanisms underlying coexistence in these congeneric stream salmonids. Analysis of the charr social networks revealed that their interspecific dominance hierarchies were highly orderly, linear, steep, and stable through time, similar to intraspecific hierarchies (Fausch, 1984; Nakano, 1994, 1995b). The dominance ranks

TABLE 2 Characteristics of the best-fitting exponential random graph models of social networks among Dolly Varden and whitespotted charr in two pools in Poroshiri Stream during two summers

Pool	Period	Edges	Nodecov (length)	Absdiff (length)	Nodematch (WSC) ^a	Nodematch (DV) ^a	Significant goodness-of-fit tests ($p < 0.05$)
A	1991	-5.574 $p < 0.0001$	0.588 $p < 0.0001$	-0.518 $p = 0.0005$	0.172 $p = 0.72$	-1.119 $p = 0.10$	4 of 45
	1992	-11.652 $p < 0.0001$	0.782 $p < 0.0001$	0.012 $p = 0.96$	-0.549 $p = 0.44$	0.861 $p = 0.62$	0 of 36
B	1991 (early)	-10.381 $p < 0.0001$	0.609 $p < 0.0001$	-0.257 $p = 0.02$	0.450 $p = 0.34$	-1.143 $p = 0.20$	1 of 38
	1991 (late)	-13.348 $p < 0.0001$	0.748 $p < 0.0001$	-0.231 $p = 0.06$	0.357 $p = 0.34$	-0.553 $p = 0.31$	4 of 48
	1992	-6.402 $p < 0.0001$	0.355 $p < 0.0001$	-0.204 $p = 0.002$	1.167 $p = 0.002$	-1.136 $p = 0.008$	4 of 49

^aCodes refer to species homophily: WSC = whitespotted charr, DV = Dolly Varden.

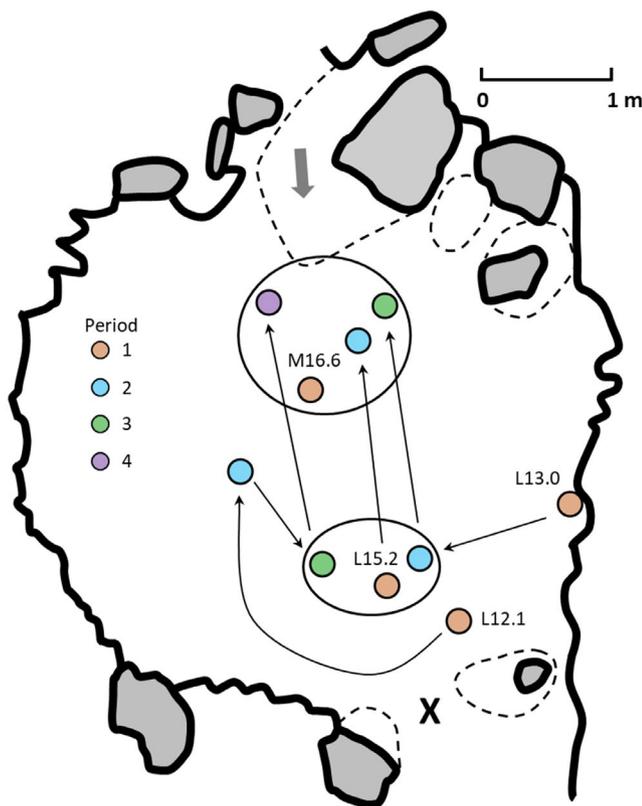


FIGURE 4 Knockout experiments in Pool A in 1991. Symbols show centroids of positions of the four most dominant fish during four periods, identified by species (M = *Salvelinus malma*; L = *Salvelinus leucomaenis*) and fork length. Ovals enclose centroids of alpha and beta fish respectively. The alpha fish was removed after each period, and arrows show movements of subordinate fish into the vacated positions. For example, the alpha fish (M16.6) held the most favourable position during period 1, and after it was removed the beta fish (L15.2) moved to a similar position and became the alpha fish for period 2. The grey arrow shows direction of flow into the pool, and X shows the observer's position at the downstream end. Dashed lines show submerged margins of key boulders

estimated using three methods were also closely correlated with ranks of fish by length. Direct determination of dominance using knockout experiments confirmed that social ranks of the 3 to 5 most dominant fish were identical to their ranks by length for all except 1 of these 17 high-ranking fish. Moreover, the ERGM revealed that larger fish were more likely to win contests, and win them against individuals of similar size that occupied the next lower ranks.

In contrast, there was no evidence that dominance was related to species identity, after accounting for body length. Fish of one species were no more likely to win contests over the other species than conspecifics, except in one case. In that case, the ERGM showed that both species were significantly more likely to win contests against whitespotted charr. However, this was expected because whitespotted charr were 2.5 times more prevalent in that pool, and so the more frequent target of interactions. ERGM are a particularly powerful tool for assessing the relative effects of size and species on interactions, because they can consider the probability of each link as functions of these covariates while accounting for all other links in the network (Silk & Fisher, 2017).

Of the two alternative hypotheses considered plausible as mechanisms promoting coexistence in this local assemblage, these findings closely match predictions of the model where interspecific competition and intraspecific competition are equal (Figure 1b). In this case, each species treats the other as the same species, and dominance is based on size alone. Our results indicate that the two species are virtually equal competitors for foraging positions in this zone of sympatry during summer. The knockout experiments also confirmed that specific foraging positions are the resource for which these fish competed, because when vacated the next most dominant fish quickly moved to occupy a similar location, even in the dynamic milieu of turbulent currents and fluctuating invertebrate drift. Moreover, although this study was conducted over a relatively short period, summer foraging is critical for stream salmonids to grow and acquire fat reserves that determine overwinter survival (e.g. Coleman & Fausch, 2007; Toney & Coble, 1980), and ultimately fitness.

Pool	Year	Mean distances between position centroids (cm)		
		Alpha	Beta	Alpha and Beta
A	1991	70 ± 22 (6)	54 ± 21 (3)	198 ± 32 (12)
	1992	38 ± 30 (3)	23 (1)	145 ± 28 (6)
B	1991 - late	76 ± 40 (10)	145 ± 96 (6)	133 ± 101 (20)
	1992	50 ± 20 (10)	117 ± 63 (6)	97 ± 58 (20)

TABLE 3 Pairwise distances between combinations of alpha and beta position centroids in four sets of knockout experiments in the study pools over 2 years. Entries are $M \pm SD$, with number of pairwise comparisons in parentheses

These results match the signature of an assemblage where effective equalizing mechanisms result in only a small difference in fitness between species, so that relatively weak stabilizing mechanisms are sufficient to overcome it and promote coexistence in zones of sympatry (Adler et al., 2007; Chesson, 2000). For example, growth, a key measure of fitness in fishes, was nearly identical for the two species over 4 years (Nakano et al., 1999). However, density of whitespotted charr was 2.4 times that of Dolly Varden, suggesting some difference in fitness owing to differences in recruitment, survival, immigration or emigration at this location. Nevertheless, the densities were remarkably stable, indicating that although these charr are apparently ecologically equivalent, they are not neutral species, for which densities are expected to vary randomly through time (McPeck & Siepielski, 2019).

This study, coupled with previous research revealed an effective stabilizing mechanism that allows individual Dolly Varden to partition food resources and avoid interspecific competition when resources are scarce, thereby overcoming the apparent disadvantage in fitness. Replicated field experiments in these same pools in 1992 showed that Dolly Varden rapidly shifted to benthic feeding when invertebrate drift was reduced with nets (Fausch et al., 1997). A 4-year observational study across a range of invertebrate drift densities in a 1.5-km segment that included this sympatric zone and the two pools revealed identical behaviours and the same switching point by Dolly Varden (Nakano et al., 1999). In contrast, few whitespotted charr shifted to benthic feeding, and only at a much lower drift threshold. In the present study, more than half of Dolly Varden had switched to benthic feeding (15 of 29, 52%), whereas only 1 of 37 whitespotted charr had shifted (3%) which is similar to the low proportion predicted by our earlier model (figure 2 in Nakano et al., 1999). Nearly 70% of the charr that switched (11 of 16) were in the lower half of their dominance hierarchies. Because dominant charr have priority in access to drifting invertebrates, subordinates occupying positions downstream and at the margins of pools are first to experience resource shortages when drift declines, and first to shift to benthic feeding. Dolly Varden are adapted for this shift owing to their more subterminal mouths, and this trait is more pronounced in sympatry owing to character displacement (Nakano et al., 2020).

The fundamental criterion for local coexistence, that each species can invade and persist when rare, is nearly impossible to test directly for mobile animals (Siepielski & McPeck, 2010). Dolly Varden density, although averaging only 29% of the age-1 and older individuals in this assemblage, remained remarkably stable, providing key

evidence of such persistence. Moreover, a snorkelling survey of 25 pools along the entire 2-km sympatric segment in August 2020 and additional angling upstream revealed the same density and identical distribution limits of both species as in 1991–1994, demonstrating coexistence over a 30-year period (S. Kitano, unpublished data). Supporting evidence necessary for coexistence includes density-dependent population regulation and trade-offs in ecological performance that prevent species from driving others from the system. Stream salmonid populations are well studied, and known to display density-dependent survival, growth and emigration (Elliott, 1994; Keeley, 2001; Nakano & Nagoshi, 1985). Growth rate is highest at foraging positions that maximize the trade-off between drift rate and cost of swimming (Fausch, 2014). This provides a logical link between the limited supply of summer foraging positions and density-dependent population demography, including emigration (Gowan & Fausch, 2002). Our previous research revealed a clear performance trade-off between these charr, driven by a behavioural shift that allows Dolly Varden to switch to benthic feeding and avoid costly agonistic interactions with whitespotted charr (Fausch et al., 1997; Nakano et al., 1999), coupled with a morphological shift to more subterminal mouths owing to character displacement (Nakano et al., 2020).

McPeck and Siepielski (2019) argue for developing a mechanistic understanding of the processes underlying community structure, by assembling observational and experimental evidence that explains why species coexist. Previous studies spanning whole-island to watershed scales (Fausch et al., 1994) coupled with laboratory and field experiments (Taniguchi & Nakano, 2000; Watz et al., 2019) showed that differences in growth and survival of these congeneric charr with temperature are a potent equalizing mechanism, resulting in relatively narrow zones of sympatry at about 7–9°C mean summer water temperature where whitespotted charr can survive but do not exclude Dolly Varden. We infer that the behavioural and morphological stabilizing mechanisms revealed by this study and previous research (Fausch et al., 1997; Nakano et al., 1999, 2020) allow Dolly Varden to maintain positive fitness in these sympatric zones despite annual declines in invertebrate drift during summer. Coupled with evidence of equal dominance for drift-foraging positions based on size alone, and equal growth and stable densities through time, these data provide a plurality of observational and experimental approaches that show how and why these two species coexist in zones of sympatry in Hokkaido streams (Siepielski & McPeck, 2010).

Finally, we note that other mechanisms operating across spatial scales may also play a role. For example, dispersal of whitespotted charr from the segment downstream might explain their higher density, or dispersal of Dolly Varden from upstream sources could result in a lower-density sink population in sympatry. However, abundant age-0 and age-1 Dolly Varden in this segment (Fausch et al., 1994; Nakano et al., 1999; K. Fausch and S. Kitano, unpubl. obs.) confirmed local reproduction, which is not characteristic of a sink population. Recent models show that the complex interplay among competitive ability, recruitment limitation, and asymmetric dispersal can promote coexistence at larger spatial scales (Figueiredo & Connolly, 2012), and these interactions deserve study in real communities.

Mechanistic approaches to understanding coexistence are relatively rare, because they require substantial ecological knowledge for particular species assemblages (Hart et al., 2018; McPeck & Siepielski, 2019). Moreover, such mechanisms have rarely been studied among animals with complex behaviours that form interspecific dominance hierarchies (Grether et al., 2013, 2017). For animals with indeterminate growth like stream salmonids where coexistence at the population scale is logistically difficult to study, the theoretical framework we present provides a useful tool to evaluate the relative strength of interspecific versus intraspecific competition. When combined with additional information on trade-offs in ecological performance based on abiotic factors and phenotypic traits, this body of evidence can contribute to a mechanistic understanding of how species coexist across habitats and landscapes.

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AUTHORS' CONTRIBUTIONS

K.D.F. and S.N. conceived the ideas and designed methods; K.D.F., S.N. and S. Kitano collected the data; K.D.F., S. Kim and Y.K. analysed the data; K.D.F. wrote the manuscript with significant input from Y.K. All living authors contributed critically to manuscript drafts and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data are archived at the Dryad Digital Repository <https://doi.org/10.5061/dryad.83bk3j9q4> (Fausch et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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