

1 **Sticklebacks show consistent prey-share hierarchies within but not**
2 **between patchy and sequential prey distributions**

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23 **SHORT TITLE: Prey distribution and prey share hierarchies**

1 ABSTRACT

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3 When animals compete, hierarchies can emerge. If the outcome of competition under different
4 conditions is dependent upon different sets of attributes, then we may expect to see hierarchies
5 that are domain-specific, rather than domain general. We tested this idea by comparing prey
6 share hierarchies within shoals of sticklebacks (*Gasterosteus aculeatus*) as they foraged for
7 patchily-distributed or for drifting prey. We found that prey share was correlated across pairs of
8 patch- and pairs of drift-foraging trials, but not between the two conditions, suggesting that
9 separate repeatable but independent prey share hierarchies arise for each for each type of prey
10 distribution. We discuss possible underlying mechanisms and ecological implications of this
11 finding.

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13 KEY WORDS: Competition; Predation; Scramble competition; Social Foraging

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1 INTRODUCTION

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3 Competition is a largely inevitable consequence of living in groups (Krause & Ruxton 2002;
4 Ward & Webster 2016). When social animals compete amongst themselves for resources or
5 dominance, hierarchies can emerge. The structure of hierarchies may be influenced both by
6 individual differences in ability to compete effectively, or through self-organising processes,
7 such as through winner and loser effects (Chase et al. 2002; Franz et al. 2015). Hierarchies form
8 in markedly different contexts, from leadership and travel initiation (Sueur 2011; Nagy et al.
9 2013), to access to mating opportunities (Chen et al. 2011), to competition over food resources
10 (David et al. 2007). The mechanisms which determine an individual's place within the hierarchy
11 may well differ between these different contexts. Ability to compete for mating opportunities
12 may be to a lesser or greater extent under hormonal control for example (e.g. Beehner et al.
13 2006; Oliveira et al. 2009) , while the ability to lead groupmates may depend more upon
14 experience, assertiveness or sociability (Flack et al. 2010; Burns et al. 2012; Ioannou et al. 2015).
15 Given this, we might reasonably predict that hierarchy structure should be context-specific.
16 Indeed, this was found to be the case in pigeons (*Columba livia*), where hierarchies based upon
17 leadership whilst in flight, and aggression during foraging were seen to be completely
18 independent of one another (Nagy et al. 2013).

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20 Travelling and foraging are clearly separate domains, but even within broad, functional contexts
21 we might expect to see a degree of condition-dependency of hierarchy structure, if performance
22 under different conditions depends upon different attributes. We explored this idea by comparing
23 the prey-share hierarchies seen within shoals of stickleback fish (*Gasterosteus aculeatus*) as they

1 compete for sequentially arriving, drifting food, and for food arranged in static patches. Previous
2 work has shown that stable prey-share hierarchies characterised by a minority of fish consuming
3 most of the prey can form and persist for several weeks in this species (Webster & Hart 2006;
4 2007). Prey intake under the scramble-competition conditions associated with drifting food
5 (Ward et al. 2006) is known to positively correlate with individual activity and boldness
6 (Webster et al. 2007; 2009). Effectively competing for patchily-distributed food may also entail
7 elements of scramble competition, however aggression may also play more of a role too; in an
8 earlier study, aggressive contest competition and kleptoparasitism rates declined over time in
9 groups held under drift foraging conditions, but remained constant when groups are presented
10 with patchily distributed prey, suggesting that these play a more important role in determining
11 prey share under such conditions (Webster & Hart 2006). In this study we tested groups of fish
12 multiple times in patch- and drift-foraging trials, predicting that prey share hierarchies would be
13 stable within patch- and drift-foraging trials, but not between them.

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15 METHODS

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17 Sticklebacks were collected from the Kinnessburn stream, St Andrews, UK using mesh traps in
18 October 2014. In the laboratory they were initially housed in groups of 40 in 90L aquaria for one
19 month. They were maintained at 8°C on a 12h light:12h darkness cycle and fed daily with
20 bloodworms. The aquaria contained a layer of gravel, artificial plants, and were equipped with
21 external filters. Following this, unsexed, non-reproductive fish were divided into 16 groups of
22 five fish each and each group was moved to its own visually isolated 45L aquarium, furnished as
23 described above. Fish within each group were familiar to one another, and were size matched to

1 within 5mm length (range across groups 35–45mm). Each fish was fitted with a non-invasive,
2 uniquely coloured 5mm diameter plastic disc tag on its left pelvic spine (Webster & Laland
3 2009). Fish were given one week to acclimate, before being tested the following week.
4

5 Each group was tested in four foraging trials, two in which the prey were presented
6 simultaneously in a single patch, and two in which the prey were presented sequentially,
7 simulating drifting food. The order of these foraging trials was randomised for each group. Both
8 patch- and drift-foraging trials were conducted in an aquarium measuring 45cmx30cmx30cm
9 (Figure 1). The aquarium contained a 1cm deep layer of sand and was filled with water to a
10 depth of 25cm. The two short sides and one long side of the aquarium were screened with black
11 plastic sheets to minimise external disturbance. A 4cm wide strip of black plastic was placed
12 above the tank down the long side with four 5mm holes placed 8cm apart to allow prey to be
13 delivered (in the drift-foraging trials only). A removable 10 cm diameter, 30 cm tall perforated
14 colourless plastic cylinder was placed against one of the short side of the tank, equidistant from
15 either longer side. This was used to hold the group of five fish prior to the start of the trial. A
16 black plastic hide was placed in front of the unscreened side of the tank. Within this we placed a
17 Logitech C600 web-camera connected to a laptop computer.
18

19 In both types of foraging trial 15 dead bloodworms were used as prey. In the patch-foraging
20 trials these were arranged within a 10cm diameter patch next to the short wall of the tank
21 opposite the starting position of the test subjects. The prey were added to the tank one minute
22 before the fish were added. The group of five fish were carefully netted from their housing tank
23 placed into the holding cylinder and allowed to settle for ten minutes. Following this, the holder

1 was gently removed from the tank, beginning the trial. The trial ran for a further 10 minutes,
2 after which the fish were removed and return to their holding tank. In the drift-foraging trials,
3 prey were introduced through the four holes in the plastic strip attached to the top of the tank
4 (described above). As in the patch-foraging trials, the group of five fish was first held within the
5 holding cylinder for 10 minutes. Following their release, we began to add the prey items. Each
6 prey item was delivered in 1cm³ of tank water using a pipette. One prey item was dropped every
7 30 seconds through one of the holes and a randomly predetermined order. The fish typically
8 consumed the prey as it sank to the bottom of the tank. After the final prey item had been
9 delivered the trial continued for a further 150 seconds, allowing the fish to find any uneaten prey,
10 giving a total trial time of 10 minutes. Each group was tested once a day over a 4 day period.
11 Immediately after being tested, fish groups were returned to their holding tanks. All were given
12 access to food after testing, in order to standardise hunger levels between trials.

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14 Statistical analysis

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16 From the trial videos we recorded the number of prey items eaten by each fish. We compared the
17 amount of food eaten per group in each of the four trials using a Friedman test. We investigated
18 whether prey share within groups varied between the four trials by calculating the coefficient of
19 variation of prey share for each group and trial, and comparing these, also using a Friedman test.

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21 With respect to stability in individual prey share, we first performed exploratory analyses by
22 calculating the Pearson product moment correlation coefficient for individual prey share within
23 groups between the two patch-foraging trials, between the two drift-foraging trials and between

1 the mean patch- and mean drift-foraging prey shares for each group, enabling us to estimate the
2 degree to which performance was repeatable across these trials. These were meta-analysed using
3 Stouffer's weighted Z method, in order to obtain a single test statistic for each comparison
4 (Whitlock 2005).

5
6 We then used maximum likelihood estimation to fit six statistical models describing variation
7 and consistency in individual foraging ability to the data on individual prey share across groups,
8 using corrected Akaike's information criterion (AICc) to select the models which best described
9 the observed patterns of prey share (Burnham & Anderson 2002).

10

11 Model 1 described our prediction that prey share hierarchies would be stable within patch- and
12 drift-foraging trials, but not between them. Models 2-5 describe alternatives to this prediction.
13 Model 2, with individual differences in prey capture ability that acted identically across both
14 foraging modes, corresponded with the alternative hypothesis that prey share hierarchies would
15 be stable both within and between foraging modes. The previous work of Webster & Hart (2006)
16 largely ruled out two other alternative predictions, namely that there would be no individual
17 differences in prey capture ability in the foraging tasks (the scenario described by our Model 3),
18 and that there would be individual differences in prey capture ability, but that these differences
19 would not be stable over time (our Model 4). Our Models 5 & 6 were a mixture of Models 1 and
20 3, in that fish were modelled as having individual differences in prey capture ability in one of the
21 foraging modes, patch or drift, but not in the other.

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1 We chose to model these various hypotheses as mixtures of multinomial distributions. Although
2 more complicated models may have provide better fits to the data, testing our hypotheses
3 required fitting individual level parameters, and as there were relatively few observations per
4 individual, we decided to use a simple family of models. The number of prey capture
5 observations was 960, 16 groups with 4 trials per group and 15 prey items per group, and the
6 number of individual fish was 80, 16 groups with 5 fish per group, for a total of 12 observations
7 per individual.

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9 Model 3 sat at one extreme where each trial by each group was modelled as coming from the
10 same multinomial distribution, and Model 4 sat at the other extreme where a different
11 multinomial distribution was posited and fitted for each trial by each group. Model 1 posited and
12 fitted two multinomial distributions for each group, one for their patch trials and one for their
13 drift trials. Model 2 posited a single multinomial distribution for each group which applied to
14 both patch and drift trials. Models 5 and 6 were a blend of Models 1 and 3, positing a single
15 multinomial distribution for all groups on patch (Model 5) or drift (Model 6) trials respectively,
16 while positing a different multinomial distribution for each group on the alternative trial type
17 (drift or patch).

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19 RESULTS

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21 Total prey intake per group did not vary across the four trials (Friedman test: $n=16$, $X^2=2.64$,
22 $df=3$, $P=0.450$). Prey share within groups was unequal but did not vary across the four trials
23 (Friedman test of coefficient of variation of individual prey intake, $n=16$, $X^2=4.90$, $df=3$,

1 P=0.179, Figure 2a & 2b). Prey share within groups was positively correlated within the pairs of
2 patch and drift trials (Stouffer's Z trend, $P < 0.001$ and 0.027 respectively). Between patch and
3 drift trials however we saw no evidence of any correlation ($P=0.751$, Figure 3).

4
5 Of the six models that we fitted to the data, Model 1 was the best supported (Table 1),
6 minimising information loss when approximating the true prey share distribution. This allows us
7 to infer with confidence that there are persistent individual differences in prey capture ability,
8 and that these individual differences in ability are distinct across food distribution types.

9 10 DISCUSSION

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12 In line with our prediction, we found prey share hierarchies to be specific to prey distribution;
13 individual prey shares were largely positively correlated within the two patch- and the two drift-
14 foraging trials, however there was little support for any relationship in prey-share hierarchy
15 between the two prey provision treatment types. Given that individual prey intake varied
16 between prey distribution treatments, it seems unlikely that individual differences in metabolic
17 rate or energy requirements alone can account for our findings. One plausible explanation for
18 this finding is that performance under different foraging conditions is determined by different
19 combinations of behavioural attributes or behavioural syndromes (Sih et al. 2004). Such a link
20 has already been demonstrated in sticklebacks, where more active and bolder individuals also
21 tend to be superior competitors under drift feeding conditions, possibly because such individuals
22 are simply more likely to encounter drifting food sooner than their less active group mates or
23 because they are more willing move into the open to reach food once they have detected it

1 (Webster et al. 2007; 2009). Boldness and activity may be less important in shaping performance
2 when competing for patchily-distributed prey, though it is interesting to note that boldness was
3 positively correlated with prey intake in sticklebacks that were tested alone (Jolles et al 2016).
4 Here then there is scope for further research that builds in the current study by identifying the
5 behavioural correlates of social foraging performance under these different conditions.

6
7 It is conceivable that resource defence may play a role in determining foraging success for
8 patchily distributed resources. Resource of food patches has been widely observed in a range of
9 species (Garber 1988; Bryant & Grant 1995; Vahl et al. 2005). It is not clear whether any form of
10 resource defence was employed by the fish in our study. We saw no differences in total prey
11 intake, nor any differences in disparity in prey share, (measured as the coefficient of variation in
12 prey intake within each group) between patch and drift prey delivery treatments, as might be
13 expected if patchy prey were defended. Moreover we saw very little evidence of contest
14 competition or overt aggression, though we note that agonistic behaviours such as these may be
15 poor indicators of the kinds of social interference effects that might limit food intake at patches
16 (Vahl et al. 2005). For species where defence of food resources by dominant individuals does
17 occur (Grant & Guha 1993; Grand & Grant 1994), prey distribution, the degree to which it is
18 clumped in space and time, is likely to have significant implications for the effectiveness of
19 resource defence strategies. Further research into the use of defence tactics across a continuously
20 varied range of prey distributions in such species would be valuable, since it would allow
21 researchers to test predictions about the effectiveness of such strategies and the flexibility with
22 which they are deployed and abandoned.

23

1 The findings of our study imply that for groups of generalist species that forage for different food
2 types, we may not be able to build an accurate picture of individual relative foraging
3 performance based upon foraging performance observed only under a narrow set of conditions.
4 Instead, it may be necessary to gather data on performance across a range of different foraging
5 types, and to take into account the competitive abilities of all group members across these, given
6 that social foraging interactions are known to depend strongly upon the combinations of
7 behavioural phenotypes present within the group (Giraldeau & Caraco 2000). A number of
8 studies have recently addressed the question of how expression of individual personality traits
9 influences and is influenced by that of the group (reviewed by Webster & Ward 2011;
10 Magnhagen 2012) and it would be useful to extend this work further by exploring the expression
11 of traits affecting food competition across different food distributions. Taking such an approach
12 may enable researchers to explain a greater proportion of the variation seen in competitive
13 interactions among social animals.

14
15 Skew theory, largely applied to competition over opportunities to reproduce, has also been
16 suggested to apply to foraging interactions; dominant individuals may punish effective
17 competitors for food resources, while poorer competitors may quit groups in order to seek better
18 access to food (Hamilton 2000). High rates of fission and fusion, coupled with low group fidelity
19 have been described for some animal groups, including some shoaling fishes (Hoare et al. 2000),
20 and it would be interesting to determine the extent to which this reflects poor competitors
21 moving between areas containing differently prey distributions or groups containing individuals
22 with different competitive abilities. Conceivably, the rules governing patch quitting likelihoods
23 invoked by classic foraging models (Charnov 1976) may also apply to group membership, with

1 individuals being more likely to switch groups if their prey intake drops below some threshold
2 level.

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4 Finally, it would be useful to determine how broadly these findings apply to other modes of
5 foraging, and more generally still, when groups of animals are faced with different tasks or
6 problems within other broad behavioural contexts, such as navigation through different types of
7 environment.

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1 REFERENCES

2

3 Beehner, J.C., Bergman, T.J., Cheney, D.L., Seyfarth, R.M. & Whitten, P.L., (2006).

4 Testosterone predicts future dominance rank and mating activity among male chacma baboons.

5 *Behav Ecol Sociobiol.* **59**, 469-479.

6

7 Bryant, M.J., & Grant, J.W. (1995). Resource defence, monopolization and variation of fitness in

8 groups of female Japanese medaka depend on the synchrony of food arrival. *Ani Behav.* **49**,

9 1469-1479.

10

11 Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical*

12 *information-theoretic approach.* New York: Springer Science & Business Media.

13

14 Burns, A.L., Herbert-Read, J.E., Morrell, L.J. & Ward, A.J.W. (2012). Consistency of leadership

15 in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. *Plos One.*

16 **7**, e36567-e36567.

17

18 Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor Popul Biol.* **9**, 129-

19 136.

20

21 Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M. (2002). Individual differences

22 versus social dynamics in the formation of animal dominance hierarchies. *Proc Natl Acad Sci.*

23 **99**, 5744-5749.

1
2 Chen, T., Beekman, M. & Ward, A.J.W. (2011). The role of female dominance hierarchies in the
3 mating behaviour of mosquitofish. *Biol Lett.* **7**, 343-345.
4
5 David, B.O., Closs, G.P., Crow, S.K. & Hansen, E.A. (2007). Is diel activity determined by
6 social rank in a drift-feeding stream fish dominance hierarchy? *Ani Behav.* **74**, 259-263.
7
8 Flack, A., Pettit, B., Freeman, R., Guilford, T. & Biro, D. (2012). What are leaders made of? The
9 role of individual experience in determining leader–follower relations in homing pigeons. *Ani*
10 *Behav.* **83**, 703-709.
11
12 Franz, M., McLean, E., Tung, J., Altmann, J. & Alberts, S.C. (2015). Self-organizing dominance
13 hierarchies in a wild primate population. *Proc R Soc Lond B Biol Sci.* **282**, 20151512.
14
15 Garber, P.A. (1988). Diet, foraging patterns, and resource defense in a mixed species troop of
16 *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour.* **105**, 18-34.
17
18 Grand, T.C. & Grant, J.W. (1994). Spatial predictability of food influences its monopolization
19 and defence by juvenile convict cichlids. *Ani Behav.* **47**, 91-100.
20
21 Grant, J.W. & Guha, R.T. (1993). Spatial clumping of food increases its monopolization and
22 defense by convict cichlids, *Cichlasoma nigrofasciatum*. *Behav Ecol.* **4**, 293-296.
23

1 Giraldeau, L.A. & Caraco, T. (2000). *Social foraging theory*. New Jersey: Princeton University
2 Press.
3
4 Hamilton, I.M. (2000). Recruiters and joiners: using optimal skew theory to predict group size
5 and the division of resources within groups of social foragers. *Am Nat.* **155**, 684-695.
6
7 Hoare, D.J., Ruxton, G.D., Godin, J-G.J. & Krause, J. (2000). The social organization of free-
8 ranging fish shoals. *Oikos.* **89**, 546-554.
9
10 Ioannou, C.C., Singh, M. & Couzin, I.D. (2015). Potential leaders trade off goal-oriented and
11 socially oriented behavior in mobile animal groups. *Am Nat.* **186**, 284-293.
12
13 Jolles, J.W., Manica, A., & Boogert, N.J. (2016). Food intake rates of inactive fish are positively
14 linked to boldness in three-spined sticklebacks. *J Fish Biol.* In Press
15
16 Krause, J. & Ruxton, G.D. (2002). *Living in groups*. Oxford University Press: Oxford.
17
18 Magnhagen, C. (2012). Personalities in a crowd: What shapes the behaviour of Eurasian perch
19 and other shoaling fishes?. *Curr Zool.* **58**, 35-44.
20
21 Nagy, M., Vásárhelyi, G., Pettit, B., Roberts-Mariani, I., Vicsek, T. & Biro, D. (2013). Context-
22 dependent hierarchies in pigeons. *Proc Natl Acad Sci.* **110**, 13049-13054.
23

1 Oliveira, R.F., Silva, A., Canário, A.V. (2009). Why do winners keep winning? Androgen
2 mediation of winner but not loser effects in cichlid fish. *Proc R Soc Lond B Biol Sci.* **276**, 2249-
3 2256.

4

5 Sih, A., Bell, A., Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary
6 overview. *Trends Ecol Evol.* **19**, 372-378.

7

8 Sueur, C. (2011). Group decision-making in chacma baboons: leadership, order and
9 communication during movement. *BMC Ecology.* **11**, 26.

10

11 Vahl, W.K., Lok, T., Van der Meer, J., Piersma, T. & Weissing, F.J. (2005). Spatial clumping of
12 food and social dominance affect interference competition among ruddy turnstones. *Behav Ecol.*
13 **16**, 834-844.

14

15 Ward, A.J.W., Webster, M.M. & Hart, P.J.B. (2006). Intraspecific food competition in fishes.
16 *Fish Fish.* **7**, 231-261.

17

18 Ward, A.J.W. & Webster, M.M. (2016). *Sociality: The Behaviour of Group-Living Animals.*
19 Springer International Publishing.

20

21 Webster, M.M. & Hart, P.J.B. (2006). Kleptoparasitic prey competition in shoaling fish: effects
22 of familiarity and prey distribution. *Behav Ecol.* **17**, 959-964.

23

1 Webster, M.M. & Laland, K.N. (2009). Evaluation of a non-invasive tagging system for
2 laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *J Fish Biol.* **75**, 1868-
3 1873.

4

5 Webster, M.M. & Hart, P.J.B. (2007). Prior association reduces kleptoparasitic prey competition
6 in shoals of three-spined sticklebacks. *Ani Behav.* **74**, 253-258.

7

8 Webster, M.M., Ward, A.J.W. & Hart, P.J.B. (2007). Boldness is influenced by social context in
9 threespine sticklebacks (*Gasterosteus aculeatus*). *Behav.***144**, 351-371.

10

11 Webster, M.M., Ward, A.J.W. & Hart, P.J.B. (2009). Individual boldness affects interspecific
12 interactions in sticklebacks. *Behav Ecol Sociobiol.* **63**, 511-520.

13

14 Webster, M.M. & Ward, A.J.W. (2011). Personality and social context. *Biol Rev.* **86**, 759-773.

15

16 Whitlock, M.C. (2005). Combining probability from independent tests: the weighted Z-method is
17 superior to Fisher's approach. *J Evol Biol.* **18**, 1368-1373.

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FIGURE LEGENDS

Figure 1. Test arena, consisting of a glass tank (a) screened on three sides with black plastic sheeting and measuring 45x30 cm, water depth 20cm. A black plastic strip (b), 4cm wide was present in both drift- and patch foraging trials. This contained four holes, at equal intervals, used to deliver prey in the drift foraging trials. A removable 10cm perforated plastic holding unit (c) was used to house the fish during the settling period at the start of the trial. In the patch-foraging trials only, prey were provided within a 10cm diameter patch, located at (d). The uncovered front of the tank was abutted by a black plastic shelter (e), containing a webcam (f), used to record the trials.

Figure 2. (a) Median prey (+/- quartiles) intake by rank (mean of both trials within each prey delivery treatment). (b) Coefficient of variation of individual prey intake across the four trials (median +/- quartiles).

Figure 3. Pearson correlation coefficients of individual prey share within groups (median +/- quartiles). To obtain median scores, individual correlation coefficients were converted to

1 Fisher's z scores. These were ranked and the 9th highest value was taken as the median, with the
2 5th and 13th highest values were used as the quartiles. These were then converted back from
3 Fisher's z scores to correlation coefficients and used to produce the figure.

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8 TABLE LEGEND

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10 **Table 1.** Support (AICc) for the six models fitted to our data. Model 1, in which feeding
11 performance was consistent within feeding modes but independent between them, was the best
12 supported.

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1 **Table 1.**

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Model	Parameters (Estimated)	Negative Log Likelihood	AIC_c	Δ (AIC_c - AIC_c*)
1. Individual, unrelated differences across modes.	192 (160)	429.38	1243.00	0
2. Individual differences, consistent across modes.	96 (80)	575.00	1324.69	81.68
3. No individual differences.	2 (1)	686.74	1375.48	132.48
4. Individual differences never consistent.	384 (320)	291.52	1543.05	300.05
5. Individual differences in Patch, but not Drift.	98 (81)	553.50	1284.09	41.09
6. Individual differences in Drift, but not Patch.	98 (81)	565.10	1307.27	64.27

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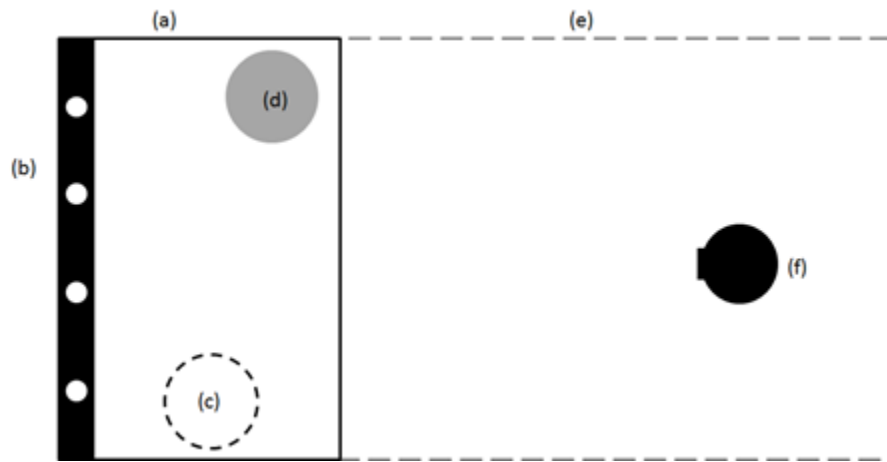
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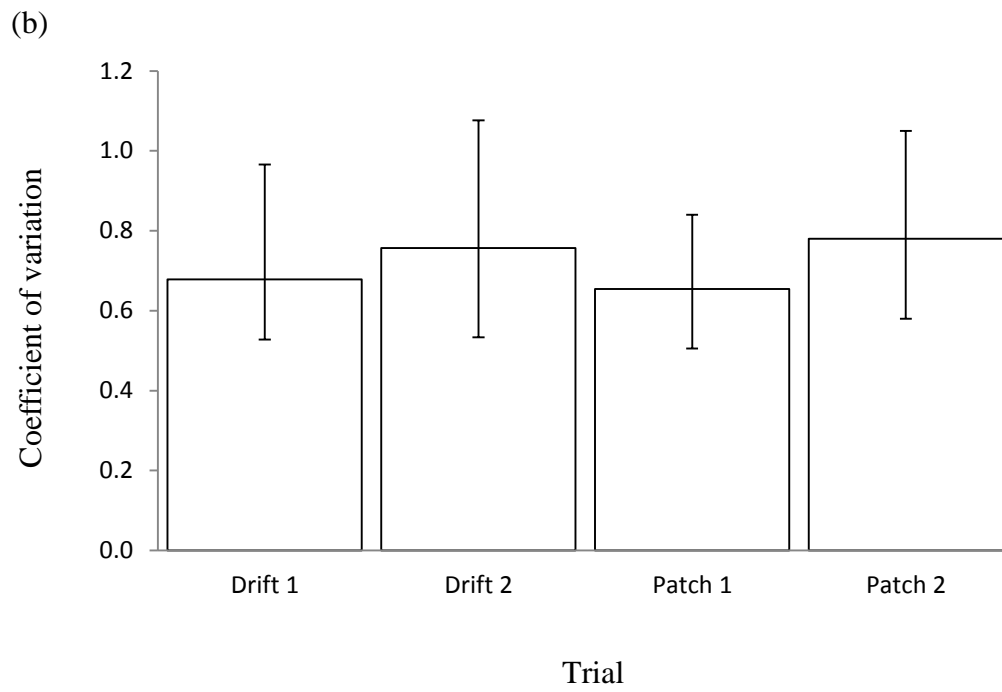
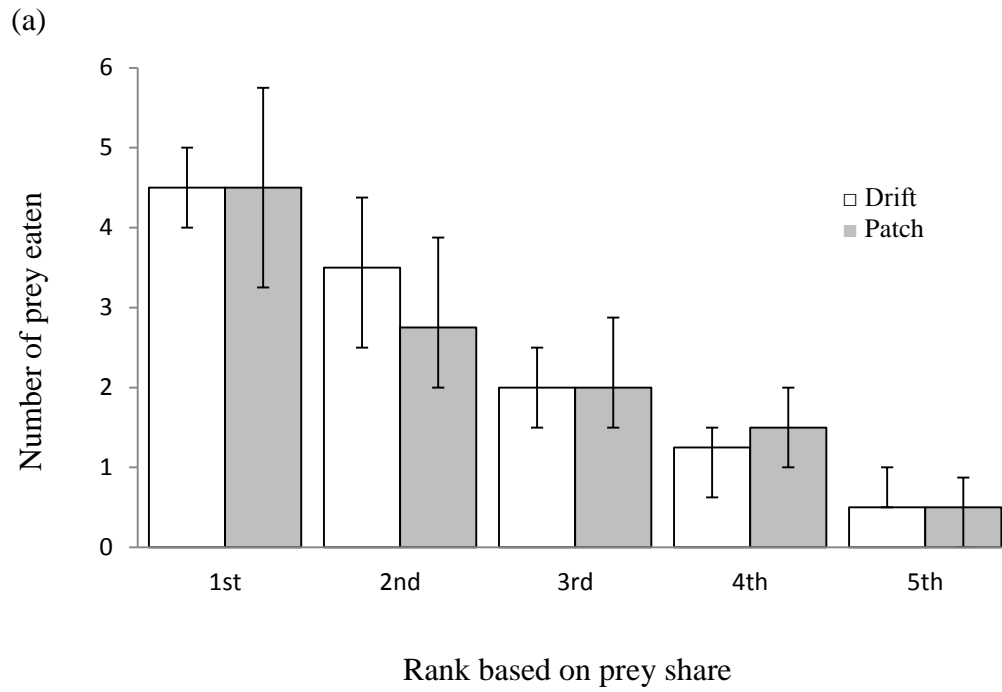
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Figure 1.



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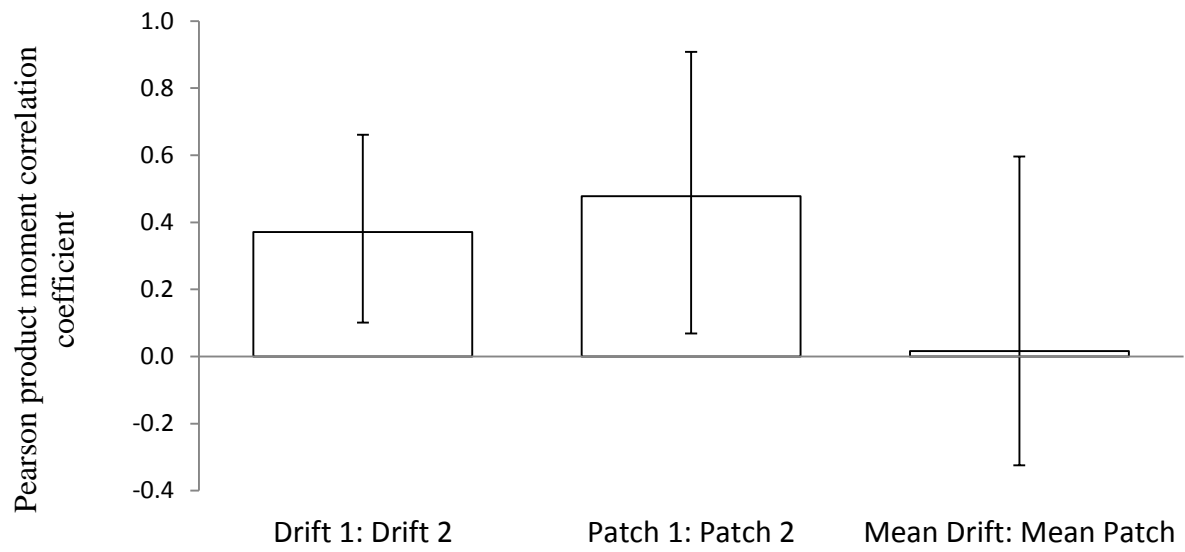
Figure 2.



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Figure 3.



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