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Effects of age and captivity on the social structure and migration survival of a critically endangered bird

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Abstract

Reintroductions of threatened species is a conservation strategy utilised around the world. Unfortunately, many translocated individuals have poor rates of survival post-release. If released individuals are unable to socially integrate into wild populations, they might lose the safety of the group or fail to learn critical skills. We examined the effects of age and captivity on sociality and migration survival for the critically endangered orange-bellied parrot (*Neophema chrysogaster*). As part of recovery efforts, adult birds are released in spring to contribute to breeding and juveniles are released in autumn prior to migration. Historically, captive-bred adults have low rates of migration survival, whereas captive and wild juveniles survive at comparable rates. We investigated both the long-term impacts of captivity on sociality and how sociality impacted migration survival by constructing social networks and comparing captive and wild birds of different age classes. We found no differences between captive and wild birds, suggesting that released birds integrated into the population. However, juveniles were more strongly connected and demonstrated greater network stability than adults. While we found no impact of sociality on survival, our results provide evidence of different migration strategies previously described for juveniles and adults: adults depart in small groups and juveniles depart as a larger flock a few weeks later. We suggest that the low migration survival of captive-bred adults may be attributable to this cohort missing the juvenile flocking phase. These results suggest that a juvenile developmental phase may be impactful in this species for future survival.

Introduction

Translocating individuals has become an increasingly important conservation strategy for many threatened populations (IUCN/SSC, 2013), yet their post-release survival is often low (Fischer & Lindenmayer, 2000; Morris *et al*., 2021). Released animals need to learn to survive in the wild quickly and the failure to acquire necessary skills can lead to poor survival outcomes (Jule, Leaver, & Lea, 2008), thus hampering recovery efforts (Seddon, Armstrong, & Maloney, 2007). While a number of variables can contribute to poor post-release survival, problems resulting from social behaviour have been identified as one of the key issues impacting translocation success (Berger-Tal, Blumstein, & Swaisgood, 2019), in part because the way animals interact can have carry-over consequences for other threats such as predation which has been documented to be a significant danger for many species (Fischer & Lindenmayer, 2000; White *et al*., 2012). For some species, successful integration into an existing group post-release has shown to be crucial for survival (Snyder *et al*., 1994), both for the safety provided by the group (Elgar, 1989) and learning important skills from wild conspecifics (Brakes *et al*., 2019).

Once integrated into a group, translocated animals can learn critical survival skills and information from social interactions, including effective foraging strategies (Farine *et al*., 2015a; Thorogood, Kokko, & Mappes, 2018), predator recognition (Swift & Marzluff, 2015) and migration behaviours (Mueller *et al*., 2013). An individual's social position can therefore impact their ability to learn new skills (Boogert *et al*., 2008; Langley *et al*., 2018), receive important information (Boogert *et al*., 2014b), or to adapt to changing circumstances (Franks *et al*., 2020b), which creates carry-over effects on fitness via diminished survival (Langley *et al*., 2020) and/or reproduction (Schubert *et al*., 2007). For example, Franks *et al*. (2020b) demonstrated that juvenile hihi (*Notiomystis cincta*) who gained more associates after translocation tended to have a higher rate of survival. Similarly, stable social relationships improved the reproductive success of female greater ani (*Crotophaga major*); females who maintained stable long-term associations fledged more chicks compared to females with less-stable social bonds (Riehl & Strong, 2018). Translocations inherently change the social structure of populations (Parker *et al*., 2012; Firth *et al*., 2017), so understanding how translocated individuals integrate into a population could help improve survival outcomes and recovery efforts (Snijders *et al*., 2017; Moseby *et al*., 2020; Brakes *et al*., 2021).

The social structure of populations is especially important when considering the introduction of captive-bred animals. Captivity inherently presents a very different early-life environment compared to the wild (Mason *et al*., 2013; Crates, Stojanovic, & Heinsohn, 2022), including reduced opportunities for social learning (Harrison *et al*., 2011; Spiezio *et al*., 2018). Furthermore, an individual's early life experience can affect social position within a population (Boogert, Farine, & Spencer, 2014a; Brandl *et al*., 2019). In this way, being born in captivity may disadvantage translocated animals if they cannot socially integrate with wild conspecifics post-release (Jule *et al*., 2008; White *et al*., 2012; VanderWerf *et al*., 2014).

Given that reintroductions of captive-bred animals are a globally important tool in the fight against extinction (IUCN/SSC, 2013), understanding the fitness consequences of social behaviour on reintroduction success is an important emerging aspect of conservation science (Goldenberg *et al*., 2019; Sosa *et al*., 2021). Social network analysis (SNA) has become a powerful tool that can reveal both the impacts of fine-scale social position on individual fitness outcomes (Formica *et al*., 2012; Beck, Farine, & Kempenaers, 2021) or expose important underlying population structures which can impact survival or reproduction (Snijders *et al*., 2017). This can be particularly important for small populations that are more sensitive to the dramatic population changes caused by translocations (Parker *et al*., 2012; Firth *et al*., 2017; Snijders *et al*., 2017). Understanding the structure and importance of social groups can therefore help inform management decisions and release protocols to help improve the translocation success (Goldenberg *et al*., 2019): for example, black-tailed prairie dogs (*Cynomys ludovicianus*) were five times more likely to survive translocation when they were translocated in family groups (Shier, 2006) and Dunston *et al*. (2017) used SNA to demonstrate that captive-bred lions were able to form social structures comparable to wild prides. However, despite increasing recognition of the importance of social structure for conservation programmes (Brakes *et al*., 2021), (and the powerful tool offered by SNA), there remain few examples using this approach to explore the relationships between release protocols, social structure and the consequences for reintroduced animals.

We investigate the relationship between captivity, social position, and survival using a model species subject to an intensive reintroduction programme. The critically endangered orange-bellied parrot (*Neophema chrysogaster*) is a small parrot that breeds in remote southwestern Tasmania during the austral spring/summer and migrates each winter to the Australian mainland before returning to the breeding grounds in spring (Brown & Wilson, 1981; BirdLife International, 2018a). As part of ongoing recovery efforts, captive-bred adults are released each austral spring with the aim of maximising the number of nests initiated in the wild (DELWP, 2016). In recent years, the recovery programme has also trialled releasing captive-bred juveniles in the austral autumn prior to migration (Pritchard *et al*., 2021). Little is known about orange-bellied parrot social structure, but parrots as a group are extremely social (Heinsohn, Buchanan, & Joseph, 2018) and juvenile orange-bellied parrots are known to form flocks prior to migration (Brown & Wilson, 1981). The threats driving the decline of orange-bellied parrots remain poorly defined and largely unmitigated but are suspected to include habitat loss, migration mortality and Allee effects (Stojanovic *et al*., 2017, 2020). Additionally, there is good evidence that first-migration survival of juvenile parrots has halved over the last two decades for unknown reasons (Stojanovic *et al*., 2020).

Adults survive the migration at a much higher rate than juveniles (approx. 58% compared to approx. 20%, [Stojanovic *et al*., 2020]), suggesting that an individuals' first migration is more perilous than subsequent attempts. While the low rate of juvenile survival is limiting population growth (Stojanovic *et al*., 2023), wild and captive juveniles are equally likely to survive their first migration attempt (Bussolini *et al*., 2023a). However, the migration survival probability of released captive-bred adults is reportedly very low (Smales *et al*., 2000; BirdLife Australia, 2020) making this group much less likely to survive their first migration compared to both juveniles and wild adults. This is surprising because the majority of captive-bred adults released in spring have already survived several months in the wild, yet few go on to successfully complete the migration (Smales *et al*., 2000; BirdLife Australia, 2020).The poor migration survival of released captive-bred adults is of conservation concern due to the extensive resources required to breed and release captive animals (Fischer & Lindenmayer, 2000).

Captivity can have long term impacts on social behaviour and position (Goldenberg *et al*., 2019; Crates *et al*., 2022) and sociality can impact individual survival in a number of ways (Boogert *et al*., 2014b; Langley *et al*., 2018; Franks *et al*., 2020b). If captive-bred adults are unable to socially integrate post-release, birds might be unable to form social bonds. This could increase mortality risks (if they are unable to benefit from the safety of the group) or impair their ability to learn information critical to migration success (including timing, migration routes and stopover points).

Furthering our understanding of survival probabilities is arguably one of the most important factors facing orange-bellied parrot conservation, as poor survival outcomes (both of released adults and the low rates of juvenile survival) undermine recovery of this critically endangered species (Stojanovic *et al*., 2023).If social behaviours contribute to poor migration outcomes for captive-bred adult parrots post-release, recovery programmes can take steps to integrate this information into management practices, adjust release strategies and help improve the fitness outcomes of translocated populations (Dunston *et al*., 2017; Goldenberg *et al*., 2019).

Given the importance of social integration during early life on fitness, we hypothesise that the low survival of captive-bred adults arises from long-term impacts of an early life in captivity. If this is the case, we predict that released captive-bred adults would show differences in their sociality compared to both wild-living adults and juveniles, whereby less integration with a flock may result in an individual experiencing a lower number of social connections, being more peripheral in a group and having more transient (and therefore variable) associations. In turn, social position could influence an individuals' probability of surviving its first migration. To determine if captivity has long-term impacts on orange-bellied parrot social position we investigated: (i) differences in the number and strength of associations, (ii) position within the network and (iii) stability of network position for different demographic cohorts. Finally, we investigated the consequences of sociality on individual migration survival outcomes. We discuss our findings in the context of management practices and reintroduction efforts that involve releases from captive populations.

Materials and methods

Background

Study species & conservation actions

The critically endangered orange-bellied parrot is a small (~45 g) parrot endemic to south-eastern Australia (Higgins, 1999). This species is an obligate migrant; birds breed in remote south-west Tasmania before migrating to the Australian mainland during the austral winter and returning the following spring (Brown & Wilson, 1981). Ongoing population decline has reduced the current breeding range to a single location at Melaleuca in Tasmania's south-west (DELWP, 2016). Birds return to the breeding grounds from late September, when they form monogamous pairs and begin nesting from mid-November – early December (Brown & Wilson, 1981). Juveniles fledge from late January – early March and stay with their parents for a few weeks before adults depart for migration (late January – early February); juveniles follow a few weeks later (BirdLife Australia, 2020) (Brown & Wilson, 1981). Birds are able to breed at approximately 9 months of age when they return to the breeding ground the following spring (BirdLife Australia, 2020).

The Tasmanian Government (NRE Tas) has facilitated an ongoing monitoring programme of the wild orange-bellied parrot population at Melaleuca since the late 1970's (Smales *et al*., 2000). Supplemental food is provided daily throughout the breeding season and these feed tables are monitored by volunteers each day from approximately September through to April (Troy & Lawrence, 2022). Thees monitoring data form the basis of both the social network and survival analyses.

A captive breeding programme was first established for the orange-bellied parrot in 1986 (Smales *et al*., 2000) and currently comprises several hundred birds across multiple institutions (Morrison *et al*., 2020). In captivity, birds are generally housed in single-sex flocks until early spring when a single male and single female are paired for breeding (Bussolini *et al*., 2023b). Breeding pairs are determined by a species coordinator to maximise genetic heterozygosity within the captive population (Morrison *et al*., 2020; Bussolini *et al*., 2023b). Juveniles are generally held with their family groups for several weeks post-fledging (BirdLife Australia, 2020).

As part of ongoing recovery efforts, captive-bred adult birds are released each spring to balance sex ratios and maximise breeding in the wild (DELWP, 2016). In recent years, captive-bred juveniles have been released in autumn just prior to migration (Pritchard *et al*., 2021). Other management actions have involved 'head-starting' by capturing wild juveniles in autumn and holding them in captivity for several months before releasing them as adults the following spring (Pritchard *et al*., 2021). At present, spring-releases of adult birds and autumn-releases of juveniles are ongoing management actions (Troy & Lawrence, 2022).

Available data

The long-term monitoring data gathered by volunteers and NRE Tas provide the basis for this analysis. Supplementary food is provided at three different locations and feed tables are monitored by volunteers for 4 h each day (see the map in the Supplementary Materials). Individual birds are recorded as present or absent during 15-min block increments throughout the 4-h daily monitoring period. Only birds that land on the feed tables are recorded. Individual birds are identified via a unique colour leg-band combination (Troy & Lawrence, 2022).

During comprehensive and long term, this dataset has some inherent limitations. Specifically, there is no indication of the length of the visit per individual and interactions are assumed (not necessarily observed) based on the occurrence of two individuals present in a given observation period. We assumed that individuals seen together in an observation period were associating in some way ('gambit-of-the-group' approach [Franks, Ruxton, & James, 2010]) as the population size is very small (17 birds returned from migration in 2016; [DELWP, 2016; Stojanovic *et al*., 2020]) and the existence of multiple feed tables means that individual parrots can choose where and when they feed, and thus with whom they associate. Additionally, there is a high degree of confidence (94%) regarding the identity and survival outcomes of each individual bird (Stojanovic *et al*., 2020), so this dataset can be considered an accurate representation of parrot social interactions in this context.

The population size of orange-bellied parrots available for detection at feed tables varies over a breeding season due to staggered arrival from migration, initiation of nesting, incubation, provisioning, fledging and migration departure; these fluctuations can result in the mean population size doubling during fledging, then halving as adults depart on migration (see the Supplementary Materials). We therefore identified an six-week period in late summer (late-January to mid-March) when the population size was relatively stable as our focus for this study. This period captured both juveniles as they entered the population (early February – mid March) and adults before they departed on migration (late January – late February; [Brown & Wilson, 1981]). This length of time allowed us to incorporate a large proportion of individuals while avoiding extreme changes in population size and preventing the network from getting too dense.

Network construction

We compiled feed table monitoring records from seven breeding seasons (2014/15–2020/21) and assembled group-by-individual matrices where all individuals recorded at the same location in the same 15-min window were assigned a unique group number. For (rare) instances of multiple unmarked individuals recorded in the same 15-min block that could not be distinguished by age or sex (2014, 2015) these observations were treated as one individual. We used the package 'asnipe' v. 1.1.16 (Farine, 2013) to build simple-ratio index weighted, undirected networks for each year which captured social interactions due to the high reliability of observing individuals in this population (Stojanovic *et al.*, 2020). All analysis was conducted in R v. 4.2.1 (R Core Team, 2023).

Aim 1: Investigating differences in social metrics

Sociability of individual birds

To investigate differences in the sociability of individual birds, we used '*igraph*' v. 1.3.5 (Csardi & Nepusz, 2006) to calculate two different metrics of social connectivity. We first calculated a value of strength (defined as the sum of a link's weight in the weighted network [Sosa *et al.*, 2020]) for each individual. Strength is a reflection of both the frequency and number of an individual's interactions and can be considered a measure of an individuals' sociality (Sosa *et al.*, 2020). As population size varied across years, we standardised individual strength within each network. To do this, we ranked individuals by their strength value and then divided the rank by the size of the population that year, so that values were bound between 0 (least social) and 1 (most social).

We also calculated a value of eigenvector centrality which measures how centrally located an individual is within the network. Eigenvector centrality can be interpreted as the amount of social support or social capital an individual has (Sosa *et al.*, 2020). Values of eigenvector centrality range between 0 (least central) and 1 (most central) and were thus comparable between networks of different sizes (Castles *et al.*, 2014). While eigenvector centrality and measures of strength can be correlated (see the Supplementary Materials) they account for slightly different aspects of the social environment (Sosa *et al.*, 2020), so we included both metrics.

Variation in network position through time

To investigate the degree of variation of an individual's social position over time, we expanded our original dataset to include 8 weeks of observations (mid-Jan–mid-March). We chose to include additional weeks in order to maximise the number of birds present in multiple time periods and increase the number of individuals that could be included in this analysis. A higher degree of variability in network position could reflect an ability to adapt and change associations more rapidly, which could be advantageous in a dynamic population as studies have shown that individuals with more adaptable social bonds do better in rapidly changing environments (Franks *et al.*, 2020b).

For each week in each year, we built simple-ratio index weighted, undirected networks using '*asnipe*' v. 1.1.16 (Farine, 2013) and calculated a value of strength for each individual within each network with '*igraph*' v. 1.3.5 (Csardi & Nepusz, 2006). Within each network we ranked individuals by their strength value. We then divided the rank by the size of the population in a given week, so that values were bound between 0 (least social) and 1 (most social). We calculated a coefficient of variation (CV) for each individual by dividing the standard deviation of an individual's standardised rank by the mean, following methodology outlined in Murphy *et al.* (2019). A lower CV indicates less variation in an individual's network position through time, while a higher CV indicates greater variability. For individual birds that appeared across multiple years, a distinct CV value was calculated for each year.

Data analysis – Social metrics

To explore how different aspects of translocation protocol linked to our three individual-level social network metrics, we then fit a series of models for each standardised ranked strength, eigenvector centrality and individual CV. We used generalised linear mixed effect models using a logit-link function and a beta distribution for both standardised ranked strength and eigenvector centrality and used linear mixed effect models for individual CV using '*glmmTMB*' v. 1.1.3 (Brooks *et al.*, 2017). We fitted as fixed effects: provenance ('wild' or 'captive'); sex ('male', 'female', or 'unknown', determined by molecular techniques [Troy & Lawrence, 2022]); age class ('adult' or 'juvenile'); how the individual entered the population in a given year ('*arrived* from migration' or '*released* from captivity'), hereafter referred to as 'release status'. We also included a three-way interaction of provenance × age class × release status to derive an estimate for each demographic cohort of interest resulting from various management actions over the timeframe of the study and investigate the full ecological framework for this species. This three-way interaction produced six distinct demographic cohorts: four adult cohorts (wild and captive adults who had arrived from migration or had been released in spring); and two cohorts of juveniles (wild and captive; please see the Supplementary Materials for a full description of each cohort).

All models included the mean-centred number of observations of each individual as a fixed effect to ensure variation was not due to differences in detection (Franks *et al.*, 2020a). Year and individual ID were included as random effects in all models to account for repeated observations of the same individual. For standardised ranked strength and eigenvector centrality, we excluded individuals with fewer than three observations (n = 39) and unknown sex (n = 5). For individual CV, we excluded individuals of unknown sex (n = 7), or individuals seen in less than two time periods (n = 55).

Model selection was based on ΔAIC >2 (Burnham & Anderson, 2002) and we evaluated model fit and verified assumptions with the 'check_model' function in '*performance*' v. 0.9.1 (Lüdecke *et al.*, 2021) and 'simulateResiduals' function in '*DHARMa*' v. 0.4.5 (Hartig, 2022). We calculated the effect sizes using '*emmeans*' v. 1.7.5 (Lenth, 2021), visualised results with '*ggplot2*' v. 3.3.6 (Wickham, 2016) and used 'performance' v. 0.9.1 (Lüdecke *et al.*, 2021) to calculate marginal and conditional and marginal R^2 values for all models.

To account for the non-independent nature of social network data and following standard analysis procedure (Franks *et al.*, 2020a; Weiss *et al.*, 2021), we used the 'network_swap' function in '*asnipe*' v. 1.1.17 to create 1000 randomised networks each with 1000 node permutations (Farine, Whitehead, & Altizer, 2015b; Farine, 2017). We then generated the same social metrics from the randomised networks (eigenvector centrality, standardised ranked strength and individual CV) and ran models with the same structures specified in the main methods section above. We then compared whether the test statistic from the real data were significantly different to the values generated from the randomised networks (see the Supplementary Materials for more details).

Assortment

As a way to determine if individuals freely socialised among the population or were preferentially associating with members of the same demographic cohort, we used the package '*assortnet*' v. 0.1.2 (Farine, 2016) to calculate an assortativity coefficient (r) between demographic cohorts for each year following methodology outlined in Firth & Sheldon (2015). Demographic cohorts were defined by an individual's provenance ('wild' or 'captive'), age class ('adult' or 'juvenile') and release status ('arrived' or 'released'). Assortativity coefficients range from −1 to 1, where positive values indicate individuals preferentially associate with others in the same cohort and negative values indicate avoidance. Assortativity analysis can reveal structure in the population that might not be detectable with social metrics alone (Newman, 2003). A high degree of assortment by demographic cohort could indicate that translocated or captive-bred birds are not integrating into the population and are preferentially associating with birds in the same cohort.

Assortativity coefficients calculated from the data were then compared against results from 10,000 randomised networks generated via node permutations sampled without replacement to account for non-independence of the network data (Firth & Sheldon, 2015; Franks *et al.*, 2020b).

Aim 2: Investigating the impact of social metrics on first-migration survival rates

Finally, we investigated the impact of social metrics on first-migration survival rates. There is a body of evidence indicating that demographic variables (e.g., age, provenance) are likely to impact survival outcomes for orange-bellied parrots, with adults having a higher estimated rate of survival compared to juveniles and captive-bred adults returning at low rates compared to other groups (Smales *et al.*, 2000; BirdLife Australia, 2020; Stojanovic *et al.*, 2020). We therefore sought to first quantify variation in first-migration survival attributable to different demographic traits. To do this, we fitted generalised linear mixed effect models with a logit-link function and a binomial error distribution using '*glmmTMB*' v. 1.1.3 (Brooks *et al.*, 2017) with individual survival outcomes as a binomial response variable and a three-way interactive term of provenance, age class and release status as a fixed effect. Year was added as a random effect. Again we fit this three-way interaction – to estimate effects for each demographic cohort of interest relative to conservation actions taken for this species.

Recapture probability in this species is very high (Stojanovic *et al.*, 2020), thus we had a high degree of confidence that all survivors would be detected in the year after their first migration. We chose to focus on first-migration survival both due to the decrease in juvenile survival rates in recent years (Stojanovic *et al.*, 2020) and to prevent individuals from appearing in the data repeatedly. This therefore excluded birds that had completed the migration previously (adult birds with a release status of 'arrived') and reduced the number of demographic cohorts to four (wild and captive adults who were released in spring and both wild and captive juveniles).

We then aimed to evaluate whether variance in sociability within demographic cohorts affected individual survival probabilities. To do this, we constructed three additional models with three different social metrics (standardised ranked strength, eigenvector centrality and individual CV) as additional interactions to the three-way interactive model (e.g., provenance × age class × release status × standardised ranked strength and so on). All models included the mean-centred number of observations of each individual as a fixed effect (Franks *et al.*, 2020a) and year as a random effect. Model selection was as stated above using AIC model selection.

Results

Investigating differences in social metrics

Sociality of individual birds

We compiled 590 records of both standardised ranked strength and eigenvector centrality for 439 unique individuals over the seven seasons. The population size within each network ranged from a low of 37 birds in the 2015/16 season to a high of 206 individuals in the 2020/21 season.

For both standardised ranked strength and eigenvector centrality, the best model based on AIC selection included the three-way interactive term of provenance, age class and release status (Table 1). For eigenvector centrality, all adults had lower estimates compared to both juvenile cohorts (Fig. 1; full model estimates are provided in the Supplementary Materials) and there was no difference in the estimates between any of the four adult cohorts (captive-arrived, wild-arrived, captive-released, wild-released). Captive-juveniles had similar but slightly higher estimates of both social metrics compared to wild juveniles. This relationship between age, provenance and release status and social metric was robust following permutations, as cohort estimates differed from those generated by randomised networks (Fig. S1). While the model for standardised ranked strength indicated similar age-provenance-release status patterns, the model permutations suggested this was not statistically robust. Estimates for both classes of juveniles and for wild-arrived adults, did not differ from random chance; instead, only captive-arrived, captive-released and wild-released adults had statistically robust estimates (Fig. S2).

Variation in network position through time

A total of 594 values of CV were calculated, comprising 449 different individuals across seven seasons. When individual CV was fitted as a response variable, the best

Table 1 List of models and AIC values for all models of (a) standardised ranked strength, (b) eigenvector centrality, (c) individual CV, and (d) first-migration survival. All models included the mean-centred number of observations as a fixed effect and year as a random effect. Models a–c also include individual ID as a random effect The preferred models for each response variable are highlighted in bold. Full model estimates are presented in the Supplementary Material

(a)	Fixed effects	*df*	AIC	Δ AIC	R^2_c	R^2_m
Standardised ranked strength	**Provenance * age class * release status + number of observations**	**10**	**−587.405**	**0.000**	**0.832**	**0.752**
	Age class + number of observations	6	−573.797	13.609	0.833	0.737
	Number of observations	5	−477.712	109.693	0.792	0.719
	Provenance + number of observations	6	−476.088	111.317	0.792	0.721
	Release status + number of observations	6	−475.943	111.462	0.792	0.720
	Sex + number of observations	6	−475.749	111.656	0.793	0.719
	Null	4	−32.057	555.348	0.347	0.000

(b)	Fixed effects	*df*	AIC	Δ AIC	R^2_c	R^2_m
Eigenvector centrality	**Provenance * age class * release status + number of observations**	**10**	**−713.638**	**0.000**	**0.858**	**0.771**
	Age class + number of observations	6	−710.276	3.361	0.861	0.759
	Number of observations	5	−522.340	191.298	0.793	0.706
	Sex + number of observations	6	−520.737	192.900	0.793	0.708
	Provenance + number of observations	6	−520.422	193.216	0.794	0.705
	Release status + number of observations	6	−520.352	193.286	0.793	0.707
	Null	4	−49.947	663.691	0.410	0.000

(c)	Fixed effects	*df*	AIC	Δ AIC	R^2_c	R^2_m
Individual CV	**Age class + number of observations**	**6**	**−81.288**	**0.000**	**0.293**	**0.200**
	Provenance * age class * release status + number of observations	10	−74.608	6.680	0.297	0.201
	Number of observations	5	−73.348	7.941	0.275	0.186
	Provenance + number of observations	6	−72.157	9.131	0.293	0.200
	Sex + number of observations	6	−72.069	9.219	0.278	0.187
	Release status + number of observations	6	−71.501	9.788	0.274	0.186
	Null	4	45.077	126.366	0.115	0.000

(d)	Fixed effects	*df*	AIC	Δ AIC	R^2_c	R^2_m
First-migration survival	**Provenance * age class * release status + number of observations**	**6**	**467.813**	**0.000**	**0.080**	**0.080**
	Provenance * age class * release status * individual CV + number of observations	10	471.487	3.673	0.102	0.102
	Provenance * age class * release status *standardised ranked strength + number of observations	10	473.471	5.658	0.088	0.088
	Provenance * age class * release status * eigenvector centrality + number of observations	10	474.125	6.312	0.089	0.089
	Null	2	477.547	9.733	0.002	0.000

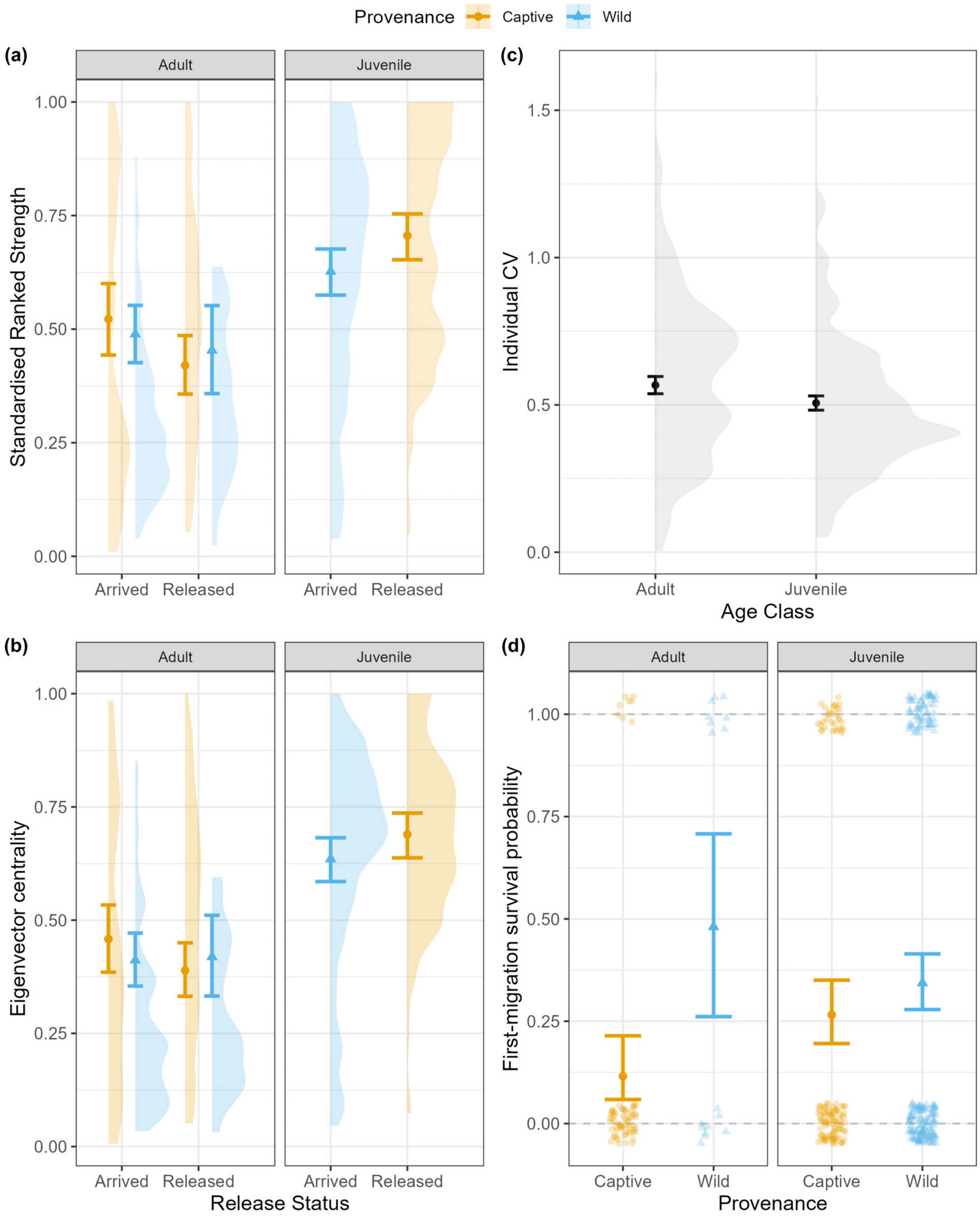

Figure 1 Model estimates (points) and 95% confidence intervals for (a) standardised ranked strength and (b) eigenvector centrality as a function of provenance × age class × release status, (c) individual CV as a function of age class and (d) first migration survival as a function of provenance × age class. (a–c) Number of observations has been included as a fixed effect, while year and individual ID have been included as random effects in all models. Density curves show the distribution of the raw data. (d) First-migration survival analysis includes both captive and wild adults released in spring and all juveniles. Year has been added as a random effect. Points show the raw data and have been vertically offset to improve visualisation.

supported model based on AIC selection included the single term of age class (Table 1). There was a small but significant difference in network variation between adults and juveniles, with adults having a higher CV and thus a greater degree of variation in social position and connections through time compared to juveniles (Fig. 1, full model estimates are provided in the Supplementary Materials). Conversely, juveniles were more stable in their social connections and positions through time. Reflecting these patterns in consistency, model estimates for the effect of adults on CV did not differ from those expected by random chance generated by permutations, while juveniles were significantly different to random (Fig. S3).

Assortment

Orange-bellied parrots showed strong positive assortment by demographic cohort, indicating that associations were the strongest between members of the same cohort and the weakest between members of different cohorts (Fig. 2). Assortativity coefficients were positive (range: 0.08–0.22) for every year and fell well outside the 95% range generated by random permutations of the dataset (Fig. 2). This suggests that orange-bellied parrots primarily associate with individuals of the same age class, release status and provenance as themselves. Mixing matrices for each year are presented in Supplemental Materials.

Impact of social metrics on the survival

A total of 396 individuals had suitable social data to be included in our analysis of first-migration survival. The best supported model for first-migration survival only included the three-way interactive term of provenance, age class and release status (Table 1). When social metrics (standardised ranked strength, eigenvector centrality and individual CV) were added as an additional interactive term, social metrics did not improve model fit based on AIC values (Table 1). This suggests that within each demographic cohort, individuals were equally likely to survive regardless of their sociality, network position, or level of variability in social interactions.

Wild adults released in spring had the highest probability of surviving their first migration (48%, CI: 26.1–70.8%), while released captive adults had the lowest (11.5%, CI: 5.8–21.5%). Captive and wild juveniles survived at similar rates consistent with other estimates of juvenile survival (26.6%, CI: 19.5–35.1% and 34.3%, CI: 27.8–41.5% respectively).

Discussion

Our study aimed to map the social structure of orange-bellied parrots to investigate potential long-term impacts of both age and captivity on social position and first-migration survival. We reveal key social differences between adults and juveniles. Juvenile orange-bellied parrots are more centrally located in the network (higher eigenvector centrality) and more stable in their network position through time (lower CV) (Fig. 3), in comparison to the less consistent adult social connections.

This highly social behaviour of juveniles could reflect known descriptions of orange-bellied parrot life history. After breeding, adult birds depart on the migration first in

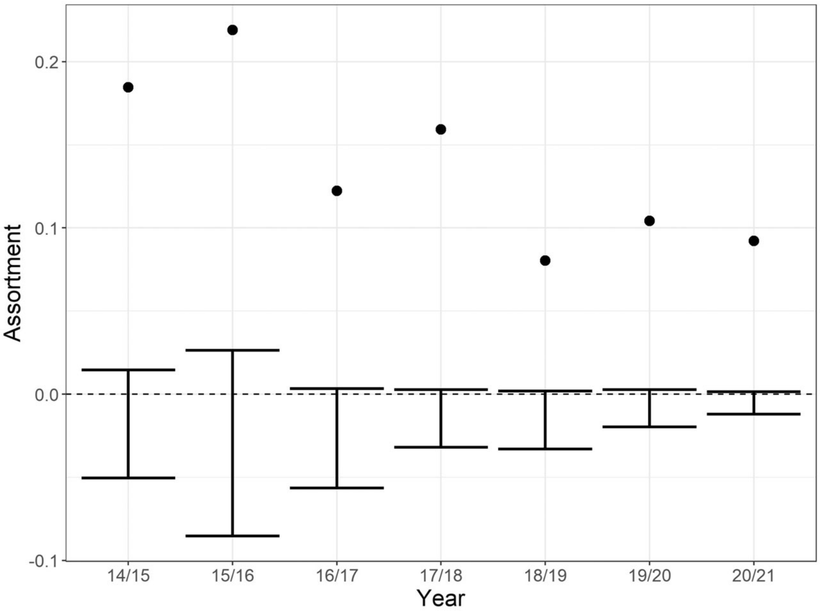

Figure 2 Coefficient of assortment (points) between different demographic cohorts (provenance × age class × release status) for each season compared against 95% range of assortment coefficients calculated from 10,000 random permutations of the data (error bars). This shows a high degree of preferential assortment between demographic cohorts, as the assortment coefficient is well above the range expected by chance.

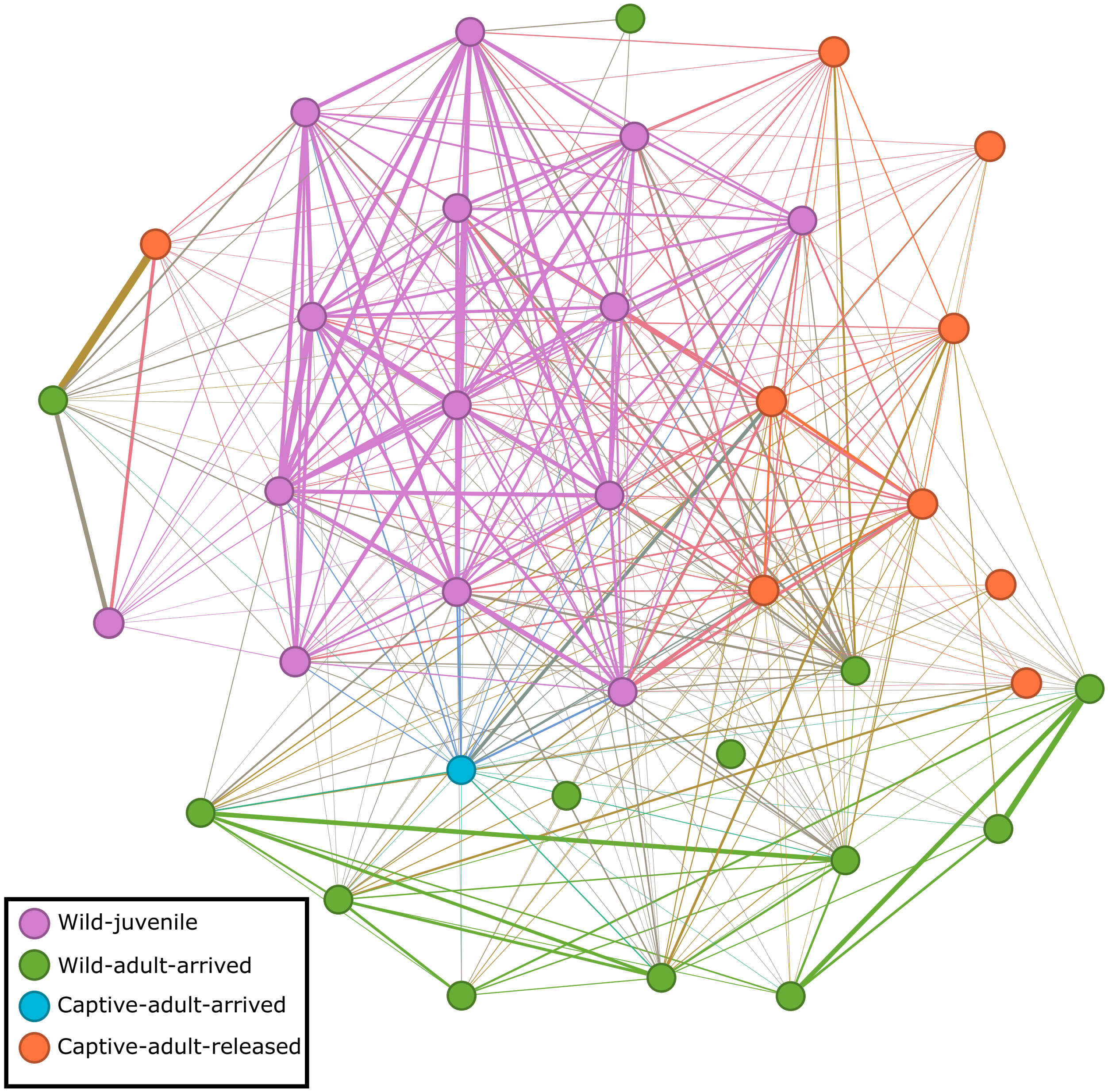

Figure 3 An orange-bellied parrot social network for a six-week period in early 2016. Nodes (points) represent individual birds and are coloured based on demographic cohorts. Edges (lines) represent co-occurrence in a group, with edge width proportional to the number of co-occurrences and coloured based on age class. This network plotted with a Fruchterman-Reingold layout.

staggered groups, leaving juveniles to flock together before they also leave a few weeks later (Brown & Wilson, 1980, 1981). The higher eigenvector centrality and network stability seen in juveniles, in addition to the high degree of assortment in the population, likely reflects this flocking behaviour, whereas the higher CV and lower eigenvector centrality could reflect the adult birds already having departed on migration. Furthermore, we detected less robust effects from standardised ranked strength (an individual's relative number of associates) in comparison to eigenvector centrality (encompassing both an individual's own *plus* its neighbour's connectedness). This warrants further investigation over further years to probe variation in different network qualities further, but could reflect a differences in sociality from being in a highly connected juvenile flock compared to more transient adult associations.

The pre-migration juvenile flocking period could involve forming important social bonds and/or learning critical skills for migration as birds can learn migration skills from conspecifics (Mueller *et al.*, 2013). If this is the case, this could explain both the similar survival rates of captive and wild juveniles and the poor survival of captive adults. Captive adults might be disadvantaged because they missed a critical juvenile learning or socialisation period. The higher first-migration survival rates of wild birds released as adults (wild-adult-released) also support this theory. These birds fledged as juveniles in the wild for a few weeks before being caught and held in captivity over winter and released in spring as adults. Despite months in captivity, these birds have a much higher rate of first-migration survival than captive-bred adults released at the same time of year, perhaps due to their early experience flocking with other juveniles. There is evidence that social disruption early in life can have profound and long-term consequences for a variety of species (Shannon *et al.*, 2013) (Brandl *et al.*, 2019; Turner *et al.*, 2021), which could potentially help explain the low migration success of captive-bred adults.

Alternatively, this period of juveniles flocking prior to migration could be about finding safety in numbers rather than learning migration skills, since more experienced adult birds have already departed on migration. Observations of migrating orange-bellied parrots by Brown & Wilson (1980) describe juveniles consistently being seen in large groups, while adult birds were usually seen in pairs or small groups. These descriptions, coupled with our findings, suggest that juvenile orange-bellied parrots form 'gangs' similar to those described in ravens (*Corvus corax*) (Dall & Wright, 2009) and hihi (*Notiomystis cincta*) (Franks *et al.*, 2020c). Juvenile lead gangs can act as information centres and provide evolutionary advantageous foraging strategies, search efficiency and social opportunities (Wright, Stone, & Brown, 2003; Dall & Wright, 2009). While neither ravens nor hihi migrate, age-dependent migration strategies have been observed in several species of bird; juveniles often exhibit different migration behaviours and delayed departure dates compared to adults (McKinnon *et al.*, 2014; Verhoeven *et al.*, 2022) and continually adjust their migration behaviours as they age (Sergio *et al.*, 2014; Verhoeven *et al.*, 2022). The patterns seen in orange-bellied parrots suggest that juveniles in highly connected social gangs prior to migration may be advantaged. Declining survival rates in this cohort may in part be due to the historically small group sizes departing on migration and related component Allee effects (Crates *et al.*, 2017; Stojanovic *et al.*, 2020).

Captive adults released in spring exhibit very similar social behaviours to other adult cohorts and survival differences appear unrelated to the social traits we measured. Research into other migratory species suggests captive-bred individuals exhibit different migration behaviours when compared to wild birds, which could be a result of genetic differences, limited physical fitness, or ignorance about appropriate migration routes (Villers *et al.*, 2010; Burnside, Collar, & Dolman, 2017). The wild and captive populations of orange-bellied parrots are genetically similar (Morrison *et al.*, 2020) and while there are some morphological differences between captive and wild birds (Stojanovic *et al.*, 2021; Bussolini *et al.*, 2023a), released adults presumably develop enough physical fitness as they have been living in the wild for several months. Alternatively, released birds could be overly reliant on supplemental food, or be unable to recognise wild food plants on migration (BirdLife Australia, 2020). Very little is known about migration of this species, so it is impossible to say what factors are contributing to the low survival of released birds without targeted research along the migration route (Stojanovic *et al.*, 2020).

Our study did not reveal any impacts of social position on survival rates within demographic cohorts. This suggests that within each cohort, individuals are equally likely to survive regardless of their sociality, centrality, or network stability. However, our study has some inherent limitations: in addition to a very small population, these observational data are relatively coarse and survival rates are so low that only a handful of individuals return in any given year (Stojanovic *et al.*, 2017). Additionally, this survival analysis only comprises a subset of individuals captured by the SNA and is not necessarily reflective of the entire population. Therefore, we cannot discount the concept of information transmission or social position impacting survival outcomes, but this was not detectable in this study, potentially due to a lack of statistical power in the four-way interactions. Although first-migration survival of captive-bred adult birds is low, captive-bred juveniles survive at similar rates to wild birds and captive-bred adults seem to adjust their behaviours to match wild birds after release. The captive population could provide opportunities to further investigate the idea of learning and information transmission in juvenile parrots, thus better equipping birds released as adults.

As more species are threatened with extinction (BirdLife International, 2018b; Rosenberg *et al.*, 2019; Lees *et al.*, 2022), conservation breeding programmes will continue to be a critical tool for recovery programmes worldwide (IUCN/SSC, 2013). Our research demonstrates that captivity does not necessarily impact sociality, but shows that captive-bred adults have much poorer survival outcomes compared to birds released as juveniles. This could imply some sort of critical learning period with significant carry over effects on fitness. These findings highlight the need to investigate the impacts of different management strategies on post-release and first-migration survival. The equivalent migration survival rates of captive and wild juveniles (Bussolini *et al.*, 2023a) support the idea that releasing juveniles is a viable strategy for supporting long-term population growth in this species compared with releasing captive-bred adults (Pritchard *et al.*, 2021; Stojanovic *et al.*, 2023). However, the contribution of released captive-bred adults has been crucial to preventing the extinction of this species by increasing breeding in the wild (Stojanovic *et al.*, 2020). Managers must balance the risks and benefits of both management strategies (Stojanovic *et al.*, 2023).

Overall, captivity can impact both social behaviour and individual fitness and this information can help recovery programmes improve the post-release survival and grow threatened populations. We have demonstrated how social network analysis can be applied in complex reintroductions scenarios to understand the consequences of social interactions when animals in the population originate from multiple sources and across years. While social metrics did not impact first-migration survival for orange-bellied parrots, differences in social interactions may still have the potential to impact longer-term measures of reintroduction success and thus still warrants further exploration in future.

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Authors' contribution

L.T.B, D.S. and V.F conceptualised the study. L.T.B. analysed the data with support from V.F and D.S. L.T.B. drafted the initial manuscript with input from all authors and supervision from R.H. and D.S. All the authors contributed to editing and reviewing the final version of the manuscript.

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Conflict of interest

L.T.B. is currently employed with the Tasmanian Government (NRE) Orange-bellied Parrot Tasmanian Programme. No other potential conflicts of interest were reported by the authors.

Data availability statement

Data were provided through a research agreement with the Department of Natural Resources and Environment Tasmania Orange-bellied Parrot Tasmanian Programme (https://nre.tas.gov.au/conservation/threatened-species-and-communities/lists-of-threatened-species/threatened-species-vertebrates/orange-bellied-parrot/the-obp-tasmanian-program) and are used with permission.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Supporting Information.