Social integration and acclimation of translocated bighorn sheep (*Ovis canadensis*)

Marc-Antoine Poirier*, Marco Festa-Bianchet

Département de biologie, Université de Sherbrooke, Sherbrooke, Canada
Centre d'Études Nordiques (CEN), Université Laval, Québec, Canada

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ABSTRACT

Translocation of animals to reinforce small populations is a widespread technique in conservation biology. Recent reviews of translocation science underline the need to monitor translocated individuals. We sought to quantify social integration within the resident population and acclimation to a new environment of translocated bighorn sheep (*Ovis canadensis*) in a wild population in Alberta, Canada. We used precise metrics to evaluate post-release sociality, behavior and growth of translocated individuals. We observed a gradual assimilation of relocated sheep in the local population through increased social network centrality and decreased avoidance of residents. Translocated sheep spent more time vigilant and increased vigilance when forming groups with local residents. The initial social integration of translocated individuals involved high rates of received aggression. Translocated sheep gained 19% less mass than residents during the first summer following translocation. Females did not give birth until the third year following translocation. Our results suggest that translocated sheep required one year to acclimate to their new environment and socially integrate into the local population. This study provides empirical quantification of both social integration and temporal acclimation processes for population reinforcement programs of large mammals. It increases our understanding of post-release processes and will assist in evaluating future conservation actions.

1. Introduction

Translocation of animals to reinforce populations of conservation concern is a widespread technique in conservation biology and wildlife management. Over the last 30 years, there has been an increase in the number of animal translocations to reinforce declining populations (Seddon et al., 2007; Seddon and Armstrong, 2016). In North America, population reinforcement accounts for 27% of all animal translocations (Brichieri-Colombi and Moehrenschlager, 2016). Despite their popularity, reinforcement programs have had low and variable success rates in the past (Fischer and Lindenmayer, 2000; Griffith et al., 1989). Application of conservation science and better management, however, increased success rates over the last two decades (Seddon and Armstrong, 2016). Recent reviews of translocation programs underlined the role of post-release monitoring of individuals in obtaining vital information on post-translocation processes (Armstrong et al., 2017; IUCN, 2013; Seddon and Armstrong, 2016). Indeed, post-release effects, including short-term increases in mortality, can strongly influence translocation success (Armstrong and Reynolds, 2012). Relocation can alter behavior as animals are stressed by capture, handling,

transportation, and the novelty of both the new environment and its resident conspecifics (Dickens et al., 2010; Letty et al., 2007). In some cases, acclimation to new environments and interactions with resident conspecifics are considered the most important of these stresses (Letty et al., 2007, 2003; Linklater et al., 2011). Few studies, however, have examined the processes underlying acclimation to new environments and integration within local populations.

Increasing evidence suggests that post-release behavior and growth of relocated individuals can determine translocation success (Snijders et al., 2017; Tarszisz et al., 2014). Quantification of behavior and growth can be particularly useful to understand the causes of variable success in translocation of long-lived species, that may require a long period of time to reproduce after translocation (Pinter-Wollman et al., 2009a). Yet, few reinforcement programs monitor the behavior or growth of translocated individuals (Champagnon et al., 2012), so that potentially critical aspects of the translocation process remain unknown. For example, in gregarious mammals, sociality can strongly affect translocation success (Gusset et al., 2006; Shier and Swaisgood, 2012; Snijders et al., 2017). After they are released in a novel environment, animals that are more socially integrated within the

resident population may better evaluate habitat quality and predation risk (Aplin et al., 2012; Griffin, 2004). Information acquired through social associations (Bonnie and Earley, 2007; Danchin et al., 2004) might consequently facilitate settlement and acclimation to the new environment (Pinter-Wollman et al., 2009b). Resident conspecifics, however, can also represent a risk for translocated individuals through aggression or competition for resources (Linklater et al., 2011; Sjoasen, 1997). Similarly to behavioral data, post-release physiological and morphological measures of relocated individuals are seldom used to assess translocations (Tarszisz et al., 2014). However, these measures can supply mechanistic explanations for how animals respond to a novel environment (Tarszisz et al., 2014; Wikelski and Cooke, 2006). In large mammals, body mass and changes in mass predict individual survival and reproduction, which are strongly linked to population dynamics (Gaillard et al., 2000). Therefore, behavioral and morphological data can provide suitable indicators for translocation success, further our understanding of post-release processes and ultimately help improve future translocations.

Bighorn sheep (*Ovis canadensis*) suffered major declines in North America following European settlement (Toweill and Geist, 1999). In the past century, over 20,000 bighorn sheep have been translocated to establish or reinforce wild populations (Brewer et al., 2014), yet only 41% of translocations were considered successful based on post-translocation population size ≥ 100 individuals (Singer et al., 2000), a number leading to likely population persistence in bighorn sheep (Berger, 1990). In this species, sociality, behavior and body growth have important fitness implications (Festa-Bianchet et al., 1997; Pelletier and Festa-Bianchet, 2006; Vander Wal et al., 2015). Therefore, post-release monitoring of behavior and growth may provide insight on individual fitness of translocated sheep, which in turn may help explain the success or failure of reinforcement programs.

We evaluated the social integration and acclimation of young bighorn sheep translocated into a wild population that stagnated at low numbers following a demographic bottleneck and inbreeding (Rioux-Paquette et al., 2011). Based on beneficial fitness effects of sociality in bighorn sheep (Vander Wal et al., 2015) and of habitat familiarity in other large mammals (Berger-Tal and Saltz, 2014; Frair et al., 2007), we expected that translocated sheep would integrate within the social system of resident sheep and acclimate to their new environment following translocation. Furthermore, due to the multiple stresses associated with relocation (Dickens et al., 2010; Letty et al., 2007), we predicted that social integration and acclimation would be gradual, with large initial effects fading over time. We were thus interested in assessing temporal differences in behavior and to document how and when translocated sheep would associate with residents. In addition, we sought to assess the possible somatic costs of relocation by comparing body mass and mass changes of translocated and resident sheep. Using local residents as a baseline for comparison, we present various evaluation methods of post-release behavior and growth to enhance the assessment of large mammal translocations.

2. Methods

2.1. Study area, translocations and general methodology

Ram Mountain, Alberta (52° N, 115° W, elevation 1080 to 2170 m), lies approximately 30 km east of the Canadian Rockies. Since 1971, individually marked bighorn sheep have been monitored and captured 2–6 times per year (Jorgenson et al., 1997). A density-dependent decline (Festa-Bianchet et al., 2003) followed by intense cougar (*Puma concolor*) predation (Festa-Bianchet et al., 2006) led to an 83% decrease in population size in 1992–2002. The population then stagnated at 40–60 sheep for six years (Rioux-Paquette et al., 2011). To reinforce the population, translocations were carried out in 2007 and 2015 (Table 1). Twelve yearlings were translocated during the first event. In 2012–2013, high cougar predation led to another sharp decline and a

Table 1
Mean age at translocation in years, sex and data collected for translocated and 'control' resident bighorn sheep to evaluate social integration and post-translocation acclimation at Ram Mountain, Alberta.

Translocation	Origin	Residency Status	n	Age	Sex	Data collected
2007	Cadomin	Translocated	12	1	5 F, 7 M	Morphological
	Ram Mountain	Resident	8	1	4 F, 4M	
2015	Cadomin	Translocated	9	1.7	8 F, 1 M	Social Behavioral
	Ram Mountain	Resident	9	1.9	8 F, 1 M	Morphological

second translocation of nine young sheep was undertaken in 2015. Relocated sheep were captured at Cadomin, Alberta (53° N, 117° W), 130 km northwest of Ram Mountain, then moved by truck and helicopter to Ram Mountain in late winter. Translocated individuals were marked with ear tags and visual collars. All bighorn sheep on Ram Mountain were individually identifiable. The second translocation was used to evaluate sociality, behavior and body mass of relocated individuals. Body mass measures were also available for the first translocation.

Social and behavioral metrics were evaluated through observations collected from late May to late September in 2015 and 2016, when sheep were observed for approximately 4 h/day. We divided each field season in two (before and after 31 July), thus providing periods of similar sample sizes to examine detailed temporal changes in sociality and behavior. To quantify social integration and acclimation, we compared behavior of the nine translocated sheep with a 'control group' of nine residents (Table 1). The 'control group' included all resident sheep of the same age and sex as relocated individuals at the time of the translocation. All analyses included as covariates the study period (1–4, corresponding to the first and second half of the May–September field seasons of 2015 and 2016), sheep residency status (translocated vs. 'control' resident) and the interaction between these variables, to test for social integration and acclimation of translocated sheep. All statistical analyses were performed in R v. 3.3.1 (R Development Core Team, 2015) and models were fitted using the *lme4* package (Bates et al., 2015). Model selection followed a backward stepwise procedure to remove nonsignificant ($p > 0.05$) fixed effects (Crawley, 2012).

2.2. Social networks

Bighorn sheep generally segregate into either nursery groups of females, lambs and yearling males or groups of males aged 4 years and older. Males aged 2 or 3 years occur in both types of group (Ruckstuhl, 1998). Since all translocated sheep were aged 1–3 years in 2015, we only considered observations of nursery groups. We used social networks, describing associations among members of nursery groups (Vander Wal et al., 2016; Wey et al., 2008), to assess the temporal variation in sociality and possible patterns of non-random associations of translocated and resident sheep. Network analyses excluded lambs, which associate closely with their mothers until weaning. Sheep seen fewer than 8 times during a study period (1.3% of sheep observed in nursery groups) were excluded from network analyses of that period. For each dyad throughout each study period, we calculated a half-weight index (HWI; Cairns and Schwager, 1987). We constructed networks weighted by the HWI using the *asnipe* package (Farine, 2013). Hypothesis testing was carried out by comparing observed social networks to random social networks generated from 10,000 data-stream permutations which sequentially swap associations between pairs of individuals observed in the same location at the same time (Farine, 2013; Farine and Whitehead, 2015). We then estimated the significance of our tests by comparing the observed statistic to the distribution of the

same test statistic generated using permutations. Use of permutations controlled for structure and non-independence in the data (Croft et al., 2011). For each period, we compared the coefficient of variation (CV) of the association indices (HWIs) of observed networks to the CVs of randomized network HWIs to test if the observed networks contained more preferred/avoided relationships than expected at random (Farine and Whitehead, 2015). Nursery group individuals were divided in three sub-groups composed of translocated, 'control' resident and 'other' (i.e. older) resident sheep. We then tested for presence of specific non-random associations by individually comparing mean HWI between sub-groups in both observed and randomized networks. Additionally, we calculated eigenvector centrality, a proxy for sociality, of all individuals in each observed and random network using the *iGraph* package (Csárdi and Nepusz, 2006). Eigenvector centrality refers to an individual's eigenvalue in the first eigenvector of the matrix of association indices. This network metric is relatively unaffected by sampling bias (Costenbader and Valente, 2003). It is a measure of how central an individual is to the network, either by being strongly linked to many others or by being directly linked to highly central individuals (Brent, 2015; Ramos-Fernández et al., 2009). In our study population, eigenvector centrality is correlated with other network metrics and with individual fitness (Vander Wal et al., 2015). To test for differences in eigenvector centrality between translocated and 'control' resident sheep, we fitted a linear model (LM) with residency status as a fixed effect for each study period (Farine and Whitehead, 2015). Comparison of model coefficients of observed and random networks then allowed to estimate the significance of residency status on eigenvector centrality.

2.3. Intra-group cohesion

In addition to social networks, which are derived from observations of group composition, we included an "intra-group cohesion index" to better quantify within-group social interactions. We thus observed foraging groups of ≥ 4 individuals. Depending on group size, every 3–5 min we scanned the entire group from left to right recording the nearest neighbour of each individual. The nearest neighbour was the sheep whose shoulders were closest to the shoulders of the focal sheep (Sibbald et al., 2005). We stopped observations if more than one-third of the group was lying down or when the group left its initial location. We calculated a cohesion index for each sheep in the group by dividing the number of times it was recorded as a nearest neighbour by the total number of times it was observed for each sampling event. This index estimated the tendency of sheep *i* to stay close to *any* other sheep in the group. If the distribution of sheep in a group is random, all sheep are expected to have the same cohesion index. Sheep that tend to avoid other sheep will obtain a lower index score, while the opposite will be true for sheep that tend to stay near other sheep. We included group size, age, sex, and reproductive status in a linear mixed model (LMM) with sheep ID and group ID as random factors.

2.4. Vigilance

To measure vigilance behavior, we recorded sheep activity during 10-minute focal observations in 2015 and 2016. We considered three behavioral states: foraging, vigilance and 'other', which included traveling, resting and social interactions. Sheep were considered vigilant when they raised their head above shoulder height (Rieucau and Martin, 2008; Ruckstuhl et al., 2003). If the focal individual lay down or was out of sight for > 60 s, the observation ended. For each observation, time spent out of sight was excluded from analysis. To calculate the proportion of time spent vigilant, we divided time spent vigilant by the sum of time foraging or vigilant. The rate of vigilance events was calculated by dividing the number of events by the time the sheep was active. For each focal observation, we noted group size and composition, including the proportion of translocated sheep, time, and location. The latter was a categorical variable of 22 distinct areas of the

mountain frequently used by sheep. The proportion of translocated sheep in the group was examined to test if individuals were more vigilant when associating with unfamiliar conspecifics. We fitted generalized linear mixed models (GLMM) with a binomial distribution and logit link function for both proportion of time spent vigilant and rate of vigilance events. Sheep ID and group location were included as random variables to control for repeated measures and unaccounted structure. Continuous explanatory variables were centered and divided by two standard deviations to allow model convergence and facilitate the interpretation of model coefficients (Gelman, 2008; Schielzeth, 2010).

2.5. Aggressive interactions

Aggressive interactions were recorded ad libitum in 2015 and 2016. Four types of interactions were noted: front kick, mount, butt and noncontact displacements (Pelletier et al., 2004). When an encounter between two individuals included repetition of the same aggressive behavior, we recorded a maximum of one interaction every 10 min. We calculated the rate of received interactions for all individuals in each period by dividing the sum of received interactions by the number of times the individual was seen. We only considered received interactions since translocated sheep were young and rarely initiated interactions (Festa-Bianchet, 1991). To compare translocated and 'control' resident sheep, we fitted a generalized linear model (GLM) with a binomial distribution and logit link function controlling for age, sex and reproductive status.

2.6. Mass gain

Translocated and 'control' resident sheep were captured 4–11 times (mean = 7.84, SD = 1.88) in the two years following translocation. Individual mass was adjusted to June 5 and September 15 using a mixed model based on individual recaptures (Martin and Pelletier, 2011). Mass gain was the difference in mass between early June and mid-September. This analysis also included 10 yearlings translocated to Ram Mountain from Cadomin in 2007 and the 8 resident yearlings present in 2007. We first compared mass of translocated and resident sheep in early June following translocation to determine any differences in mass prior to summer mass gain. Using a linear model (LM), we compared summer mass gain of translocated and resident sheep of the same age-sex classes for both translocations events (2007 and 2015) in the two years following translocation. Sex and June mass were included in the model. We controlled for year and translocation event as fixed factors because there were only 2 levels for each (Bolker et al., 2009).

3. Results

3.1. Translocations

In 2007, there were 42 resident sheep. Of twelve yearlings translocated, only five survived at least two years and settled on Ram Mountain. The two females that stayed first gave birth at age 4, in the fourth year following translocation.

In 2015, there were 43 resident sheep, in addition to one ram and two ewes translocated in 2007. The nine translocated sheep represented an increase of 19.6% in population size, and all survived to 2017. One 3-year-old ewe was pregnant during translocation. She gave birth but her lamb died overwinter. None of the translocated sheep reproduced until 2017, when six of eight females, aged 3–5 years, gave birth, in the third year following translocation.

3.2. Social networks

In 2015–2016, we recorded 3735 sightings, including 747, 918 and 2070 of translocated (Trans), 'control' resident (Control) and 'other' resident (Other) sheep, respectively. All translocated females were seen

Period 1

Period 2

Period 3

Period 4
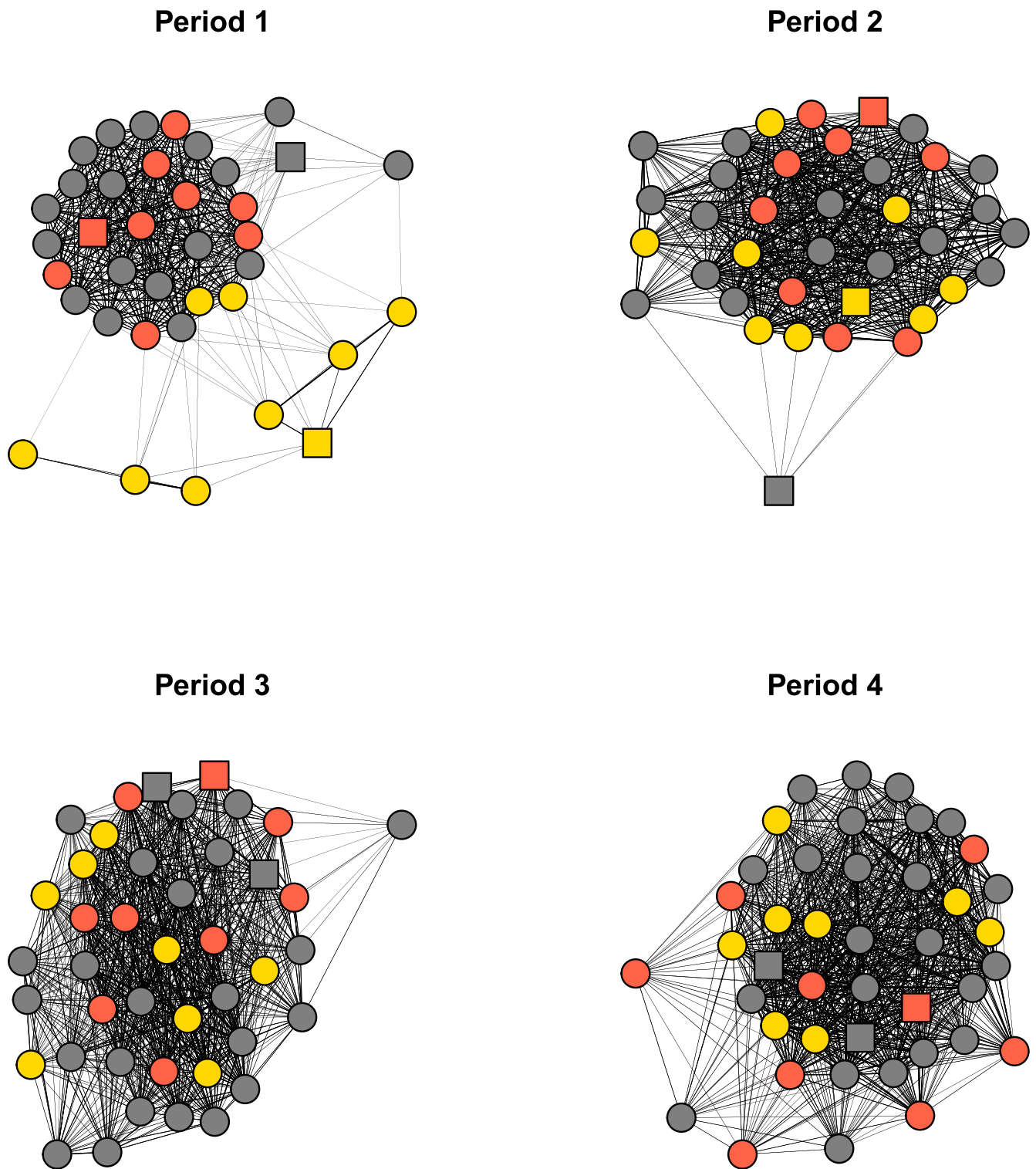
Fig. 1. Social networks of bighorn sheep nursery groups on Ram Mountain in 2015 and 2016 based on half-weight indices (HWIs). Network nodes represent individuals and connecting edges denote social associations. Networks include translocated (yellow), resident 'control' (red) and other resident (grey) sheep. Networks for each of the four study periods, consisting of the two halves of the two field seasons after translocation, are represented. Females and young males are indicated by circles and squares, respectively. Edge thickness is proportional to association strength (HWI). Only HWIs > (mean HWI) / 2 are represented to ease visualizing networks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

associating with residents at least once in each study period (Fig. 1). However, after the second period, the young male, by then aged 2, only associated with adult males (Fig. 1). Comparison of observed and randomized network CVs indicated that sheep associated non-randomly in

all periods (Fig. A1). In the first period, translocated sheep preferentially associated with each other and avoided residents (Table 2). This pattern then gradually faded, so that there was no avoidance of resident sheep by Period 3 and no preference for other translocated

Table 2
Preferred (+) and avoided (−) associations between groups of sheep over four study periods according to permutation tests based on HWIs. Preferred or avoided associations were deemed significant when the mean association index differed from that expected from a random distribution ($p < 0.025$ in all cases). Sub-groups are translocated (Trans), resident 'control' (Control) and 'other' residents (Other).

Period	Dates	Trans–Trans	Trans–Control	Trans–Other	Control–Control	Other–Other	Control–Other
1	May 30–July 31, 2015	+	−	−	+	+	n.s.
2	Aug 1–Sept 22, 2015	+	−	n.s.	+	+	n.s.
3	May 30–July 31, 2016	+	n.s.	n.s.	n.s.	n.s	+
4	Aug 1–Sept 24, 2016	n.s.	n.s.	+	n.s.	n.s	n.s.

sheep by Period 4 (Table 2). Mean eigenvector centrality of translocated sheep was lower than that of residents during the first study period, but not significantly different in subsequent periods (Table A1; Fig. A2).
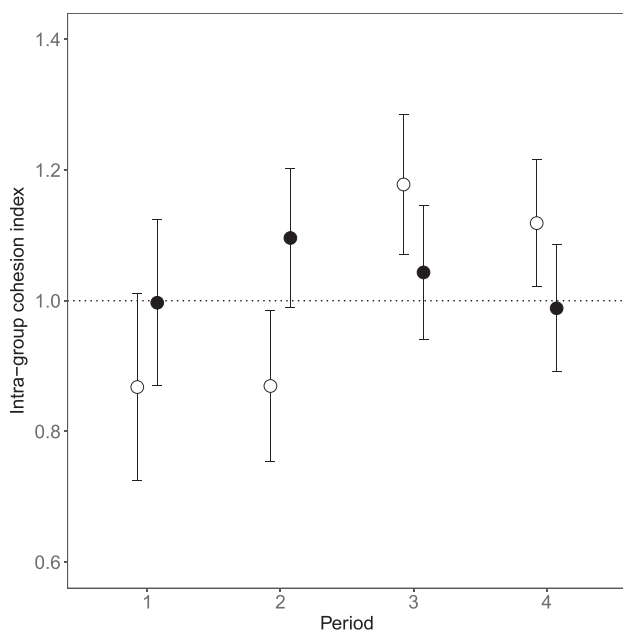
3.3. Intra-group cohesion

In 2015–2016, we recorded cohesion indices during 73 sampling events, which lasted on average 17:42 min (± 6:52 SD). Mean and median number of scans for each event were 4.6 (SD = 1.56) and 5, respectively. Compared to residents, translocated sheep tended to avoid other sheep during the second period (Table A2; Fig. 2). However, we observed the inverse trend in Periods 3 and 4, when translocated sheep tended to stay closer to other sheep within a group (Table A2; Fig. 2).

3.4. Vigilance

A total of 44.5 h of observations were carried out during 321 focal observations of the 18 translocated and 'control' sheep. Mean and median duration of focal observations were 8:18 (± 2:13 SD) and 10:00 min, respectively. Translocated sheep were more vigilant than residents in the first two periods, but this difference faded over time (Table A3; Fig. 3). In the first period only, translocated sheep increased vigilance when associated with more resident sheep (Table A3; Fig. 4). Resident sheep increased vigilance in groups with translocated sheep. (Table A3; Fig. 4). The selected model also included a negative effect of
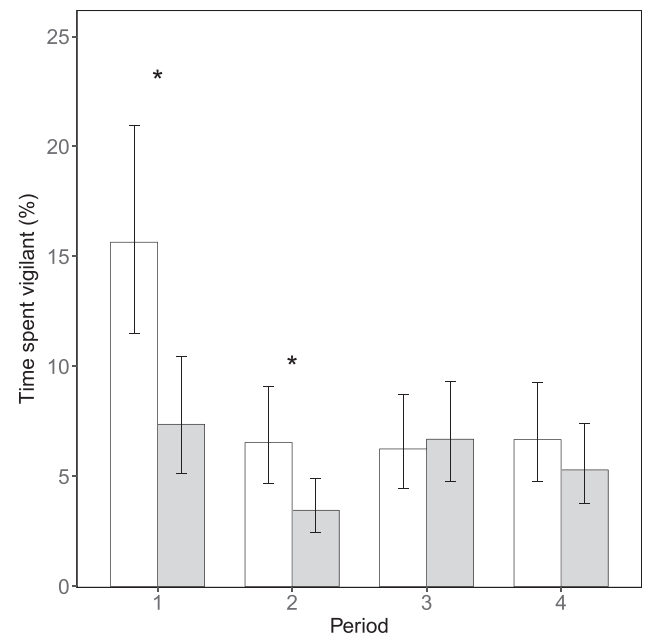
Fig. 3. Percentage of time spent vigilant by bighorn sheep on Ram Mountain, 2015 and 2016, over four study periods. Means and their 95% CIs are shown for translocated (open bars) and resident (filled bars) sheep. Significant differences are indicated by asterisks.

Fig. 2. Intra-group cohesion index of translocated and resident bighorn sheep for each study period. Periods 1 and 2 are the two halves of the field season (late May to September) following translocation, Periods 3 and 4 are the two halves of the second field season. Means and their 95% CIs are given for translocated (open dots) and resident (filled dots) sheep.
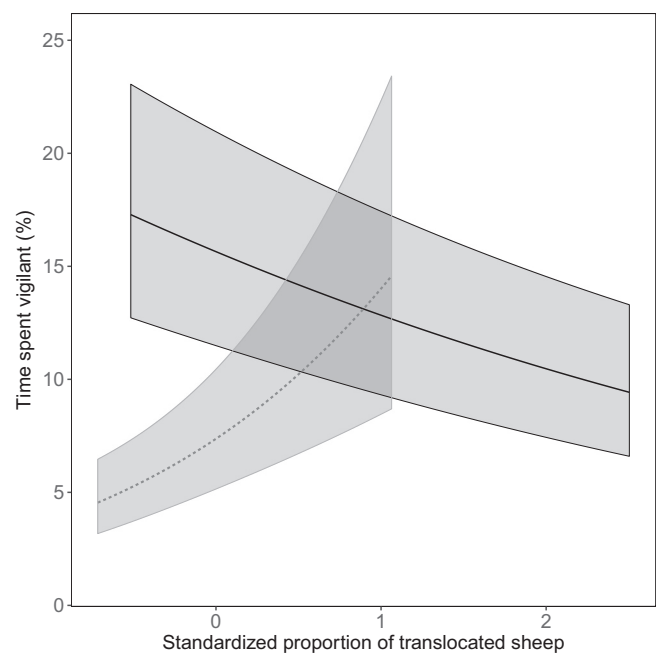
Fig. 4. Percentage of time spent vigilant in relation to the proportion of translocated bighorn sheep in the group from May 30 to July 31 in the year of the translocation. Translocated (filled line) and resident (dotted line) sheep are represented with their 95% CIs (error bars).
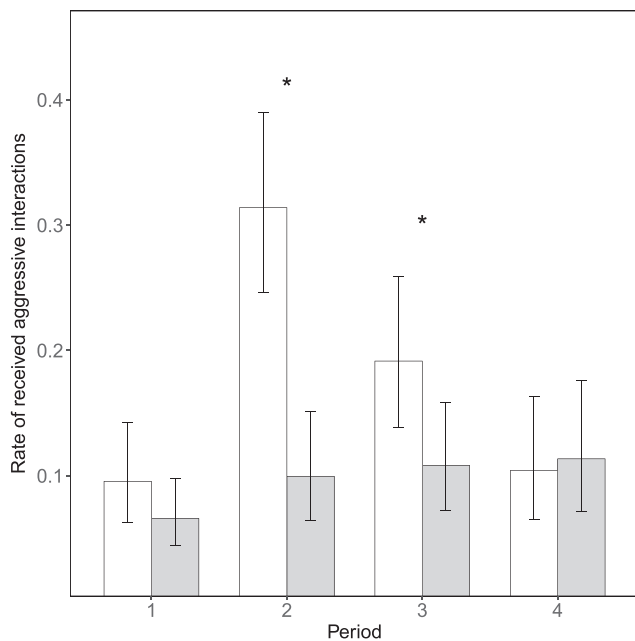
Fig. 5. Rate of received aggressive interactions (sum of received interactions/number of times the individual was seen) by bighorn sheep on Ram Mountain over four study periods. Means and their 95% CIs (error bars) are given for translocated (open bars) and resident (filled bars) sheep. Significant differences are indicated by asterisks.

group size and a quadratic effect of time of the day (Table A3). Translocated sheep were also vigilant more often than resident sheep in the first two periods (Table A4, Fig. A3).

3.5. Aggressive interactions

In 2015–2016, the 18 translocated and 'control' sheep were seen 1665 times (mean = 92.2, SD = 15.8) and received 220 aggressive interactions (mean = 12.2, SD = 8.5). On average, translocated sheep received more aggressive interactions than resident sheep in Periods 2 and 3 (Table A5; Fig. 5). In these periods, translocated sheep also appeared to receive more aggression from translocated conspecifics (15.5%) than did 'control' residents (4.6%). Younger sheep received more aggressive interactions, regardless of their residency status (Table A5).

3.6. Mass gain

Combining the 2007 and 2015 translocation events, we measured 67 summer mass gain values for 36 bighorn sheep, including 19 translocated and 17 resident sheep. For yearlings (n = 36), mass adjusted to June 5 in the year of translocation did not differ between translocated (mean = 35.0 kg, SD = 7.3) and resident (mean = 36.7 kg, SD = 9.2) sheep ($t_{15.777}$ = 0.90, p-value = 0.38). Mean summer mass gain of translocated yearlings was 19.4% less than that of resident sheep (Table 3; Fig. 6), but no difference was observed in the following year (Table 3; Fig. 6). Mass gain was higher in 2007 than 2015 for both translocated and resident sheep. Mass in June did not predict mass gain for either translocated or resident sheep. For the 2007 translocation, survival of translocated sheep was correlated with mass gain: sheep that disappeared gained 13.7% less mass than those that remained on Ram Mountain (disappeared: mean = 12.9 kg, SD = 3.9; established: mean = 15.0 kg, SD = 2.8).

4. Discussion

Using detailed data on behavior and mass of translocated individuals, we quantified post-release social integration and acclimation in wild bighorn sheep. Changes in sociality, behavior, mass, and the comparison of these measures to the resident population suggest that relocated sheep required one year to acclimate to their new environment and socially integrate into the local population.

Using a network approach, we documented a gradual assimilation of relocated sheep in the local population through increased centrality and decreased avoidance of residents. Similarly, translocated Alpine ibex (*Capra ibex*) needed 1–2 years to fully associate with resident conspecifics (Scillitani et al., 2012). Although translocated sheep joined groups with residents after the first study period, they tended to avoid other sheep within a group until their second summer on Ram Mountain. Our intra-group cohesion index agrees with the observed patterns of avoidance obtained through network analyses, and supports the conclusion that translocated sheep did not fully integrate into the local population until at least six months after translocation.

The delayed social integration of translocated sheep has important implications for the success of translocations. Early-life social associations are linked to future survival and reproductive success (McDonald, 2007; Stanton and Mann, 2012). Furthermore, in our study population, association behaviors provide direct fitness benefits primarily through adult female survival and lamb production (Vander Wal et al., 2015). These long-term consequences of sociality on fitness suggest advantages of strong and numerous social associations. For instance, familiarity with conspecifics may decrease the time allocated to both antipredator and social vigilance (Favreau et al., 2015; Griffiths et al., 2004), leaving more time for other activities such as foraging. This supposition is supported by our results. Translocated sheep, which were less social in the first two study periods, spent more time vigilant and increased their vigilance when forming groups with local residents, suggesting possible costs of social novelty. Similarly, in kangaroo rats (*Dipodomys stephensi*), translocated individuals spent less time fighting and more time foraging if they were relocated with familiar neighbors (Shier and Swaisgood, 2012). Moreover, social integration of translocated sheep at Ram Mountain led to high rates of received aggression. In black rhinoceros (*Diceros bicornis*), post-release mortality of translocated individuals was largely due to intraspecific fighting (Linklater et al., 2011). In bighorn sheep, agonistic interactions determine social rank, which in turn predicts male reproductive success (Hogg and Forbes, 1997) but provides unclear benefits to females (Favre et al., 2008). These combined social and behavioral results underline the post-release obstacles faced by translocated individuals. They may also explain the relatively poor success of the 2007 translocation for which, unfortunately, no detailed behavioral data are available.

Marked behavioral dissimilarities between relocated and resident individuals in the first year following translocation were reflected in body mass differences. Our results suggest that lack of familiarity with the resident population and a possible deficit in knowledge about the local environment (Letty et al., 2007; Scillitani et al., 2013) resulted in relocated sheep gaining about 20% less mass than residents in the summer following translocation. These results are consistent with a study that simultaneously observed somatic costs and differences in behavior for translocated African elephants (*Loxodonta africana*; Pinter-Wollman et al., 2009a). However, in the second year following translocation, we observed no differences in body mass gain. Pinter-Wollman et al. (2009a) suggested that post-release body condition may take longer to change and adjust than behavior, but for bighorn sheep mass gain deficits ceased when translocated sheep integrated within the social structure of the resident population. Differences in body growth may partially explain these different results. Unlike bighorn sheep, growth in size and mass of African elephants is slow and continues well into adult life (Lee and Moss, 1995). Nonetheless, the early mass gain deficit of translocated sheep may reduce reproductive success and longevity over the long term (Marcil-Ferland et al., 2013). Indeed, for both translocation events, relocated females did not give birth before the third year following translocation. Age of primiparity of

Table 3
Parameter estimates for the selected linear model of the determinants of summer mass gain for bighorn sheep (n = 67) in the two years following translocations in 2007 and 2015 at Ram Mountain, Alberta. 'Resident, 'Year1', 'Event1' and 'No Lamb' are the reference levels for the Status, Year, Translocation Event and Reproductive Status (RS) variables, respectively.

Full model				
Status × Year + Status × Event + June mass + Age + Sex + RS				
Final model	**Estimates**	**SE**	**T-Value**	***p*-Value**
Intercept	16.021	2.539	6.309	< 0.001
Status	− 3.969	1.056	3.759	< 0.001
Year	12.553	4.090	3.069	0.003
Translocation event	− 2.343	0.902	2.597	0.012
June mass	0.112	0.073	1.521	0.134
Status: year	− 4.170	1.611	2.589	0.012
June mass: year	− 0.329	0.093	3.545	< 0.001
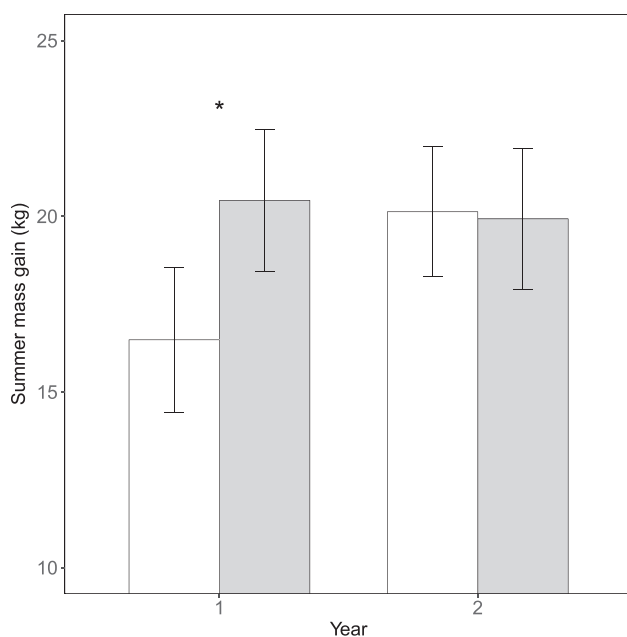
Fig. 6. Summer mass gain of translocated (open bars) and resident (filled bars) bighorn sheep for the year of translocation and the following year. Means and their 95% CIs (error bars) are represented. Significant differences are indicated by asterisks.

translocated females was about 1–2 years older than for age-matched 'control' females, suggesting a cost of early mass deficit (Martin and Festa-Bianchet, 2012). During the 2007 translocation, sheep that died or disappeared within two years of release had gained about 14% less mass during the first summer than relocated sheep that remained on the mountain. These results are in accordance with a large body of literature that underlines the importance of mass and changes in mass for large mammals (Gaillard et al., 2000). It remains unclear, however, if delayed reproduction and mortality were mostly due to changes in mass, lack of integration and acclimation, or a combination of morphological and behavioral factors.

Using a multidisciplinary approach and 'control' residents as a baseline for comparison, we uncovered details about the temporal acclimation and social integration of translocated individuals. For example, the apparent absence of behavioral differences in group cohesion and received aggressive interactions in the first study period arose because most translocated sheep did not associate with residents during that period. Without a network analysis, it would have been difficult to correctly interpret these results. Furthermore, our approach revealed individual variation in social integration, since two of the nine relocated sheep integrated into the local population during the first

period (see Fig. 1). Individuals that integrated rapidly also received more aggression, likely explaining why most relocated sheep avoided residents until the third period. These individual differences might have important long-term implications and provide further understanding of post-release processes. Further investigation of how short-term sociality, behavior and growth of translocated individuals may predict long-term fitness and translocation success is needed in bighorn sheep. For translocated swift foxes (*Vulpes velox*), post-release movement behavior predicted future reproductive success (Moehrenschlager and Macdonald, 2003). Similarly, post-release foraging and aggressive behavior of translocated kangaroo rats partially explained future survival and reproduction (Shier and Swaisgood, 2012).

Although the social and behavioral aspects of this study involved only nine translocated individuals, that sample size is representative of recommended numbers to reinforce declining populations of similar size to the bighorn sheep population at Ram Mountain. For the genetic rescue of Florida panthers, it was suggested that eight young females be translocated from Texas to the local population of approximately 40 breeding adults (Hedrick, 1995). A larger number of translocated individuals may risk swamping local genetic variation (Hedrick and Fredrickson, 2010).

Overall, our analyses show that social integration and post-release acclimation are simultaneous, based on social, behavioral and morphological measures. Our results lead to specific conservation and management recommendations for reinforcement programs of bighorn sheep. First, if the main goal is demographic rather than genetic rescue, we suggest translocating a higher proportion of females. Females are usually primiparous at 3–4 years (Martin and Festa-Bianchet, 2012) and can produce an offspring every year afterwards. Males, on the other hand, need to acquire a high social rank to mate. This rank is strongly correlated with age and mass (Pelletier and Festa-Bianchet, 2006), so that the initial stress and reduced mass gain associated with translocation may have more long-lasting effects on the reproductive success of males than of females. Second, since sociality plays an important role in adult survival and reproduction (Vander Wal et al., 2015), we suggest releasing groups of young individuals so post-release effects may dissipate by the time they reach reproductive age. In this study, translocated females began to reproduce 1–2 years later than expected for age-matched resident females. Therefore, managers should expect a minimal demographic contribution from translocated individuals for two years post-release, and account for that expectation in population projections. In the absence of more species-specific information, we suggest that these recommendations also be used for ungulate species with similar social structures. As the number of translocations increase in response to local population declines, post-release monitoring of growth, behavior and reproduction can improve translocation techniques. Our results contribute to our understanding of post-release processes and will assist in evaluating future translocations.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2017.11.031.

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