Chick and juvenile survival of Japanese rock ptarmigan Lagopus muta japonica

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Original article

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Atsushi Kobayashi & Hiroshi Nakamura

We estimated clutch size, hatching success, chick survival before independence from hens and juvenile survival after independence in Japanese rock ptarmigan *Lagopus muta japonica* during 2006-2012 on Mt. Norikura, Honshu, Japan. The tame behaviour of this subspecies provided us a unique opportunity to observe them at a close range throughout the period from hatching to adulthood. The average clutch size was 5.7 ± 0.1 ($\pm$ SE). We estimated the average hatching success to be 0.602 ± 0.880, the average nest hatching success to be 0.733 ± 1.071, the average hatchability of successful nests to be 0.907 ± 0.017 and average female survival during June, as an indicator of their survival during laying and the incubation periods, to be 0.905 ± 0.055. We attributed all egg losses to predation by carnivores. Clutch size, nest success, hatchability and female survival during June did not vary among years. Chick survival decreased sharply during the first four weeks of the brooding season. The average annual chick survival until independence was 0.278 ± 0.097, but it varied from 0.096 ± 0.051 to 0.639 ± 0.084. Survival of juveniles after independence was higher than for chicks before independence. Average over-winter survival of juveniles was larger and was 0.902 ± 0.015. We estimated the average reproductive success of Japanese rock ptarmigan from egg-laying to one year old to be 0.586 ± 0.883 birds/breeding female. Weather conditions, especially rainfall, during the first two weeks of the brooding season appeared to negatively affect chick survival.

Key words: chick survival, clutch size, hatching success, Japanese rock ptarmigan, juvenile survival, Lagopus muta japonica, management, total reproductive success

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The rock ptarmigan *Lagopus muta* has a large distribution within which the species is found in two primary environments, arctic and subarctic areas above 60°N, and in alpine areas in North America, Europe and Japan (Johnsgard 1983). Because rock ptarmigans are adapted to extreme environmental conditions, they are considered to be a sentinel species for evaluating species' responses to environmental change (Martin & Wiebe 2004, Sandercock et al. 2005). Although the rock ptarmigan is not globally threatened, southern populations of small sizes and geographically isolated may be at conservation risk (Storch 2000).

The Japanese rock ptarmigan *L. m. japonica* is the southernmost subspecies of rock ptarmigan and occurs on the island of Honshu in central Japan (Nakamura 2007). They have been declining for > 30 years because of increasing predation, habitat loss and impacts from tourism development (Haneda et al. 1985, Nakamura 2007). Climate change may pose a threat in the future as it does for other alpine populations (Storch 2000, Nakamura 2007).

Because Japanese rock ptarmigan have no fear of humans, we were able to observe and count birds at a close range (Nakamura 2010). Despite this relatively unique situation, very few demographic studies of

this subspecies have been conducted. Nevertheless, such information is necessary for conservation planning of this declining subspecies. Therefore, we studied annual variation of reproductive success and the ecological factors related to survival of Japanese rock ptarmigan to close this gap of knowledge.

Material and methods

Study area
We conducted our study during 2006-2012 on Mt. Norikura (36°06'N, 137°32'E) within the Chubu-Sangaku National park, which is located in the center of the distribution of the Japanese rock ptarmigan. Our study area was 14 km² with elevations ranging from 2,600 to 3,026 m a.s.l.. There were five cover types in our study area: 1) shrub dominated by creeping pine *Pinus pumila*, 2) dwarf shrub dominated by alpine azalea *Loiseleuria procumbens*, *Arcterica nana* and black crowberry *Empetrum nigrum var. japonicum*, 3) snow-patch vegetation characterised by aleutian mountainheath *Phyllodoce aleutica*, aleutian avens *Sieversia pentapetala* and *Potentilla matsumurae*, 4) alpine meadows and 5) rock outcrops (Miyawaki et al. 1969, Kobayashi & Nakamura 2011). Our study area is isolated from other alpine habitats. The ptarmigan populations nearest to our study population were about 25 and 21 km away. As we never observed marked birds on Mt. Norikura on other alpine areas, we believe that our study population was demographically closed (Nakamura et al. 2003, Nakamura 2007).

Field methods
We monitored ptarmigan by colour marking individuals on Mt. Norikura beginning in 2001. However, here we report detailed observations which we conducted throughout the breeding season (April-November) during 2006-2012. We captured unmarked birds by using a noose pole (Zwickel & Bendell 1967). We waited until chicks weighed ≥ 300 g before capturing them in early September. We marked each bird with a unique combination of two-coloured plastic rings on each leg and a numbered aluminum band. Once captured, we recorded weight, sex and age of the birds. We distinguished sexes by differences in plumage (Nakamura 2007). If we could not distinguish sex of chicks, we classified them as unknown; we changed this classification later on when we observed them at an older age. We classified

grouse as chicks, juveniles or adults. We classified all dependent birds as chicks, independent juveniles from brood breakup until one year old and all others as adults. We distinguished ages of adults and juveniles based on pigmentation patterns of primaries 9 and 10 (Weeden & Watson 1967).

We walked our study area in a manner such that we covered the whole area searching for marked and unmarked birds during April-November. It took several days to search the whole area for complete coverage. When we found marked individuals, we recorded their exact location using a Global Positioning System, vegetation at the site, flock size and sex of individuals. We identified colour bands using binoculars or direct observation if birds were within three metres. During our study, birds moved between breeding and wintering areas, but we surveyed them only on their breeding areas during April-November. We estimated the size of the territories of all of the mated males and females, and the location of their territories, each year in May and June. Throughout the breeding seasons in 2006-2012, > 90% of breeding grouse in each year were marked birds (H. Nakamura & A. Kobayashi, unpubl. data).

Nests were found mainly when females were incubating eggs because finding nests when females were laying was difficult as females covered their eggs with needles, moss or other vegetation after leaving their clutch to feed. So we found nests by finding feeding females during incubation and then following them back to their nest. We distinguished incubating females from non-incubating females by observing their feeding rate. If the number of peck times was > 100/minute, we judged them to be incubating, because feeding rate is much faster when females must return to nests than when they do not (Omachi Alpine Museum 1992, Nakamura 2006). Once we found a nest, we counted the eggs and marked the nest by placing a dead 1-m tall branch near the nest. We visited nests 1-2 times/week. Nests were considered successful if at least one egg hatched. We also considered the nest successful if we found chicks with the hen that laid the clutch, or if we found piped eggshells that were divided into two parts in the nest cup. We also recorded the number of unhatched eggs that remained in the nest cup. We classified a nest as predated if all eggs were gone or there were broken eggshells around the nest. If the entire clutch was gone, we assigned the predation to red fox *Vulpes vulpes* or marten *Martes melampus*, but if there were broken eggshells with holes in them, we assigned the predation to ermine *Mustela erminea*.

We counted chicks within broods every week until late September when broods broke up. However, on a few occasions, we were unable to conduct weekly counts because of inclement weather or other factors. Thus, we recorded the number of chicks with specific hens multiple times during the brooding season. When we found a brood, we approached it slowly and counted the number of individuals multiple times to derive the 'exact' number of chicks with each marked female.

Estimation of demographic parameters

We estimated annual clutch size, median date of hatching, hatching success, weekly chick survival and juvenile survival until one year old. Clutch size, hatching success and juvenile survival was estimated during 2006-2012, but chick survival was estimated only during 2008-2012 because of insufficient encounter data before 2008.

We estimated clutch size at onset of incubation. We estimated median hatching date in each year from the nests of known actual hatching date and estimated the others from the size of chicks in broods accompanying hens. We estimated hatching success based on three factors: nest success, hatchability and survival of females during June as an indicator of survival during the laying and incubation periods. We used the Mayfield method to estimate nest success in Program MARK version 3.1 (White & Burnham 1999). We estimated nest success only during the incubation period, because our method of nest detection could not estimate it accurately during the laying period. The incubation period of Japanese rock ptarmigan has been reported to be 22 days (Omachi Alpine Museum 1992). We estimated the incubation stage when we found the nest by estimating the date of initiation of incubation. We estimated nest success during the incubation period by raising the daily survival rate to the 22th power. We estimated hatchability as the proportion of eggs hatched successfully/clutch. This proportion was estimated only for successful nests. We estimated female survival during June from marked females confirmed alive in May and in subsequent monthly encounter data. To estimate the apparent survival rate, we analysed mark-recapture data using the Cormack-Jolly-Seber model in Program MARK. This model consisted of two parameters: the probability of surviving the interval (φ) and the probability of reencounter (p). We structured our encounter history as detected by resighting (1) or not detected (0) by resighting. We created a global model

of mark-recapture data as φ and p were dependent on season and year. We then estimated hatching success as nest success x hatchability x survival of female during June.

We estimated weekly chick survival throughout the brooding season. We defined the start of weekly periods as the first day we observed chicks in each year. We could not identify individual chicks, but we could estimate the number of chicks with each marked female each week. Thus, we created a weekly encounter history for each chick by assuming its association with marked females. Thus, if the number of chicks with specific females diminished from occasion (t) to occasion (t+1), the lower number of chicks justified classifying them as dead between each occasion. If chicks disappeared within an observation occasion (t), we included them as dead during that encounter occasion (t). We used the Burnham model in Program MARK to estimate chick survival (Burnham 1993). In this model, the fate of the individual is governed by four probabilities: 1) the probability of surviving the interval (S), 2) the probability of being found dead and reported ('justified' dead in our study; r), 3) the probability of fidelity to the sampling region (F) and 4) the probability of reencounter, conditional on being alive and in the sampling region (p). Because some years had different encounter occasions, we analysed each year separately. We fixed F to 1.0, because we surveyed our entire alpine area, and females with broods did not move far from their territories and feeding areas around the territories during the brooding season (H. Nakamura & A. Kobayashi, unpubl. data). We created a global model as survival rate (S), reencounter probability (p) and recovery probability (r) dependent for week (t), and site fidelity (F) was fixed to 1.0. If the model, which included p or r depending on week, was selected as the best model, we then calculated their average value.

Once we could no longer determine juvenile survival under the above model (i.e. after brood breakup), we used another model to estimate juvenile survival. We defined juvenile survival as the probability that juvenile ptarmigan survived from October, just after brood breakup, to one year of age in July of the following year. We used the Cormack-Jolly-Seber model because we believed that our study population was demographically closed (see section Study area). The encounter history consisted of three scenarios: 1) between brood breakup and migration to wintering areas (primarily during October), 2)

winter season (November-April) and 3) the first breeding season until one year of age (May-June). In this analysis, because we had the same encounter occasions each year, we pooled all individuals. We created a global model of mark recapture data as φ and p were dependent for season (t) and year (y).

We defined the total reproductive success as the number of birds that survived until one year of age/breeding female, which we estimated from multiplying clutch size, hatching success, annual chick survival and annual juvenile survival. To estimate average total reproductive success, we used the average value of each parameter, but we only estimated annual total reproductive success during 2008-2011 because there was a lack of chick survival in 2006 and 2007, and therefore these years were not included in the encounter data in 2013 to estimate juvenile survival in 2012.

We used the Akaike's Information Criterion corrected for small sample (AIC_c) to rank models (Anderson & Burnham 1999). We considered the model with the lowest AIC_c to be our best model, and we used the difference in AIC_c between best model and the other models (ΔAIC_c) to evaluate the relative support of each model. We followed Burnham & Anderson's (2002) advice when drawing inference about models, where models < 2 ΔAIC_c units of the top model were considered competing models and indicated strong support for a given model. We also calculated the Akaike weights for each model. These weights were summed to 1.0 and can be interpreted as the weight of evidence in favour of each model (Burnham & Anderson 2002). We analysed the daily survival rate of nests and female survival during June using *post hoc* comparisons of survival in Program Contrast (Hines & Sauer 1989). We also analysed annual difference in clutch size and hatchability. We analysed clutch size and hatchability using program R version 2.15.0, and tested it using Tukey's test and a contingency test, respectively.

Meteorological data

We conducted a Pearson correlation to assess the relationship between chick survival and specific weather variables (mean temperature during daylight, rainfall and a weather condition index). These data were recorded by the Institute for Cosmic Ray Research, University of Tokyo, located at an elevation of 2,770 m a.s.l. in our study area. We estimated the temperature during daylight as an average from recordings taken at the 06:00, 09:00, 12:00, 15:00 and 18:00. We recorded rainfall as the amount of rain in mm falling during each 24-hour period. Our weather condition index was the average of three visual recordings each day. We created a visual score of weather as follows: clear (0 point), cloudy (1 point), misty (2 points) and rainy (3 points). We conducted correlation between weekly chick survival rate estimated in the above-mentioned model and each weekly meteorological value. As our estimation of chick survival covered only five years (2008-2012), we conducted the correlation from the data pooled for every two weeks from hatching.

Results

Clutch size and hatching success

We found 72 nests which were all placed under creeping pine (Table 1). We found five nests during the laying period and 67 after that incubation had started. The clutch size varied from two to eight, and the mean clutch size for the seven years was 5.7 ± 0.1

Table 1. Annual variation in clutch size (mean ± SE) and hatching success (estimate ± SE) of the rock ptarmigan on Mt. Norikura, Honshu, Japan, with sample size (N) given in parenthesis.

Year	Cluth size	Median hatching date	Daily survival rate	Nest success	Female survival during June	Hatchability	Hatching success
2006	6.3 ± 0.3 (12)	7/6	0.989 ± 0.009 (11)	0.785 ± 2.746	0.952 ± 0.149 (21)	0.862 ± 0.045 (58)	0.644 ± 2.256
2007	5.8 ± 0.2 (11)	7/14	0.983 ± 0.011 (11)	0.693 ± 2.643	0.832 ± 0.135 (51)	0.830 ± 0.058 (42)	0.479 ± 1.827
2008	5.6 ± 0.4 (12)	7/12	0.986 ± 0.010 (12)	0.735 ± 2.690	0.921 ± 0.110 (51)	0.980 ± 0.019 (56)	0.663 ± 2.429
2009	5.4 ± 0.4 (12)	7/10	0.992 ± 0.008 (12)	0.836 ± 2.753	0.887 ± 0.085 (78)	0.927 ± 0.036 (52)	0.688 ± 2.266
2010	5.8 ± 0.3 (8)	7/8	0.979 ± 0.015 (8)	0.621 ± 2.923	0.801 ± 0.124 (65)	0.903 ± 0.053 (31)	0.449 ± 2.116
2011	5.3 ± 0.3 (9)	7/13	0.972 ± 0.019 (8)	0.537 ± 2.809	0.984 ± 0.170 (53)	0.923 ± 0.049 (30)	0.488 ± 2.553
2012	6.0 ± 0.6 (8)	7/7	0.994 ± 0.011 (8)	0.876 ± 4.135	0.899 ± 0.093 (38)	0.925 ± 0.042 (40)	0.728 ± 3.439
Total	5.7 ± 0.1 (72)	-	0.986 ± 0.004 (70)	0.733 ± 1.071	0.905 ± 0.055 (357)	0.907 ± 0.017 (309)	0.602 ± 0.880

Table 2. Model selection results for weekly survival, recapture probability, recovery probability and fidelity of rock ptarmigan chicks on Mt. Norikura, Honshu, Japan. All candidate models in this study are shown in each year.

Year	Model name	AIC$_c$[1]	ΔAIC$_c$[2]	Akaike weight[3]
2008	S_{time},p.,r_{time},f_{fixed}[4]	806.375	0.000	0.914
	S_{time},p.,r.,f_{fixed}	812.417	6.042	0.045
	S.,p.,r.,f_{fixed}	819.056	12.681	0.000
2009	S_{time},p_{time},r_{time},f_{fixed}	823.634	0.000	0.686
	S_{time},p_{time},r.,f_{fixed}	825.219	1.584	0.311
	S.,p.,r.,f_{fixed}	846.138	22.504	0.000
2010	S_{time},p.,r_{time},f_{fixed}	368.731	0.000	0.995
	S_{time},p_{time},r_{time},f_{fixed}	379.416	10.684	0.005
	S.,p.,r.,f_{fixed}	401.818	33.087	0.000
2011	S_{time},p.,r_{time},f_{fixed}	1209.815	0.000	0.815
	S_{time},p_{time},r_{time},f_{fixed}	1212.818	3.003	0.182
	S.,p.,r.,f_{fixed}	1259.511	49.696	0.000
2012	S_{time},p.,r_{time},f_{fixed}	563.550	0.000	0.700
	S_{time},p_{time},r_{time},f_{fixed}	565.247	1.698	0.299
	S.,p.,r.,f_{fixed}	643.976	80.426	0.000

[1] AIC$_c$ = Akaike Information Criterion corrected for small sample size.
[2] ΔAIC$_c$ = difference between AIC$_c$ of best model and this model.
[3] Akaike weight = the weight of evidence in favour of each model.
[4] Subscripts define parameterisation of S (survival rate), p (recapture probability), r (recovery probability), f (fidelity, fixed equal to 1), 'time' = varied for week, '.' = same value throughout brooding season.

($\pm$ SE). There was no difference in clutch sizes among years (Tukey's test: $F_{1,65}$, P = 0.326).

We checked 70 of 72 nests to estimate hatching success. The median hatching date varied each year by only about one week (see Table 1). Prior to hatching, 15 nests were lost to predation; seven were taken by red fox and three by ermine. We were unable to determine the predator of five nests.

The average daily survival rate of nests was 0.986 $\pm$ 0.004 (0 $\pm$ SE) and varied from 0.972 $\pm$ 0.019 to 0.994 $\pm$ 0.011 (see Table 1). There was no difference in daily survival rates among years (χ^2 = 1.87, P = 0.93). The average nest success was 0.733 $\pm$ 1.071 and varied from 0.537 $\pm$ 2.81 to 0.876 $\pm$ 4.14 (see Table 1).

The average hatchability of eggs was 0.907 $\pm$ 0.017 and varied from 0.830 $\pm$ 0.058 to 0.980 $\pm$ 0.019 (see Table 1). There was no difference in hatchability among years (χ^2 = 10.23, P = 0.11). All unhatched eggs remained in the nests after hatching and none disappeared.

The average adult female survival during June was 0.905 $\pm$ 0.055 and varied from 0.801 $\pm$ 0.12 to 0.984 $\pm$ 0.17 (see Table 1). There was no difference in female survival during June among years (χ^2 = 1.25, P = 0.97). Hatching success (nest success x hatchability x female survival during June) averaged 0.602 $\pm$ 0.880 and varied from 0.449 $\pm$ 2.116 to 0.728 $\pm$ 3.439 (see Table 1).

Chick and juvenile survival

We marked 745 grouse during 2001-2011 (257 chicks, 139 juveniles and 349 adults). We estimated survival of 131 chicks with 25 females, 135 with 42, 79 with 23, 168 with 40 and 111 with 21 during 2008-2012, respectively. The best models for chick survival in 2008, 2010, 2011 and 2012 indicated that weekly chick survival (S) and recovery probability (r) were dependent for week, and the reencounter probability (p) was constant (Table 2). On the other hand, the best model with all parameters being dependent for week was selected in 2009. There was a competing model in 2009 and 2012, but the Akaike weight of the best model was more than twice that of the next-best model. We estimated a constant reencounter probability (p)=0.515 in 2008, 0.529 in 2010, 0.320 in 2011 and 0.448 in 2012, and an average reencounter probability (p̂) of 0.403 in 2009. The average recovery probability (r̂) was 0.259 in 2008, 0.183 in 2009, 0.191 in 2010, 0.305 in 2011 and 0.170 in 2012.

We estimated the average annual chick survival (0.278 $\pm$ 0.097) from all top models in Table 2. The chick survival dropped to < 0.5 during the first four weeks of the brooding season except in 2008 (Fig. 1).
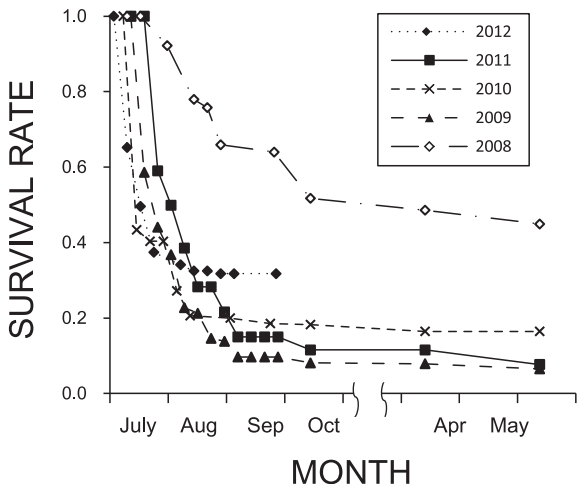

Figure 1. Annual variation in survival of Japanese rock ptarmigan from hatching to next breeding season on Mt. Norikura, Honshu, Japan. The 95% CI for each value was not included to avoid confusion in the figure (see Fig. 2 and Table 4 for CIs).

Table 3. Model selection results for apparent survival (φ) and recapture probability (p) of juvenile of rock ptarmigan on Mt. Norikura, Honshu, Japan.

Model name	AIC$_c$[1]	ΔAIC$_c$[2]	Akaike weight[3]
φ$_{time,year}$,p.[4]	1204.616	0.000	0.883
φ$_{time,year}$,p$_{time,year}$	1209.009	4.393	0.098
φ$_{time}$,p$_{time}$	1213.000	8.384	0.004
φ.,p.	1230.495	25.879	0.000

[1] AIC$_c$ = Akaike Information Criterion corrected for small sample size.
[2] ΔAIC$_c$ = difference between AIC$_c$ of best model and this model.
[3] Akaike weight = the weight of evidence in favour of each model.
[4] Subscripts defined parameterisation of φ and p: 'year' = varied among years, 'time' = varied for season.

After the fifth week, the chick loss was relatively low compared to the first four weeks. Annual chick survival probability in 2009, 2010 and 2011 was < 0.2 and was lowest in 2009 (0.096 ± 0.051; see Fig. 1). On the other hand, the annual survival in 2008 was the highest (0.639 ± 0.084; see Fig. 1).

The best model for juvenile survival indicated that survival varied by season and year, and the reencounter probability was constant (Table 3). There were no competing models. Reencounter probability (p) was 0.517 for all years and seasons.

Juvenile survival was relatively high compared to chick survival (see Fig. 1 and Table 4), and survival was particularly high during the winter season (see Table 4). The average survival during October was 0.829 ± 0.058, but varied from 0.591 ± 0.124 to 1.000 ± 0.000. On the other hand, the average survival from November through the next April (winter season) was 0.952 ± 0.010 and was > 0.902 ± 0.015 in each year. The monthly survival during winter was > 0.983 ± 0.004 in all years. The survival during May through June (0.779 ± 0.050) was less than during the winter season. The average annual juvenile survival (survival during October-June) was

0.614 ± 0.058 but varied from 0.449 ± 0.114 to 0.890 ± 0.140.

Total reproductive success
The estimated average total reproductive success of Japanese rock ptarmigan was 0.586 ± 0.883 birds/ breeding female (average clutch size x average hatching success x average annual chick survival x average annual juvenile survival; i.e. $5.7 \times 0.602 \times 0.278 \times 0.614$). The annual total reproductive success was 1.519 ± 6.29 birds/breeding female in 2008, 0.243 ± 0.812 in 2009, 0.430 ± 2.035 in 2010 and 0.203 ± 1.070 in 2011.

Relationship between chick survival and weather
Chick survival was correlated with weather conditions during the initial first two weeks of the brooding season (Fig. 2 and Table 5). In particular, chick survival was negatively correlated with rainfall. In addition, variation (± SD) in survival was negatively correlated with rainfall during the first two weeks of the brooding season (r = -0.846, P = 0.001). For example, the survival during the first week in 2010 was the lowest (0.434 ± 0.111) when the weekly rainfall was the greatest (421.2 mm) and had the largest variation (± 86.3) among five years (see Fig. 2). On the other hand, in 2008 and 2011 there was little rainfall (38.0 mm in 2008 and 3.8 mm in 2011) and low variation (± 7.3 in 2008 and ± 0.9 in 2011) with good weather conditions during the first week, and the high survival was correlated with these conditions (1.000 ± 0.000). During the second week of 2011, there was a large rainfall event (of 256.0 mm) and the survival dropped to 0.590 ± 0.055. However, after the third week, the variation in chick survival did not seem to be correlated with weather condition such as in the 11th week in 2011 when there was a high survival and also a large amount of rain fell

Table 4. Annual variation of juvenile survival with sample size (N), apparent survival (Φ) and standard error apparent survival (SE) shown of Japanese rock ptarmigan on Mt. Norikura, Honshu, Japan.

| Year	October				November-April				May-June			
	N	Φ	SE	95% CI	N	Φ	SE	95% CI	N	Φ	SE	95% CI
2006	14	1.000	0.000	1.000-1.000	46	0.904	0.025	0.844-0.943	53	0.912	0.136	0.272-0.997
2007	21	0.591	0.124	0.346-0.799	30	1.000	0.000	1.000-1.000	39	0.760	0.111	0.421-0.932
2008	38	0.810	0.098	0.549-0.938	82	0.939	0.016	0.899-0.965	101	0.924	0.097	0.445-0.995
2009	19	0.838	0.111	0.509-0.963	32	0.975	0.023	0.664-1.000	41	0.827	0.137	0.420-0.969
2010	14	0.987	0.154	0.000-1.000	26	0.902	0.015	0.818-0.949	32	1.000	0.000	1.000-1.000
2011	11	0.786	0.164	0.349-0.962	21	1.000	0.000	1.000-1.000	27	0.667	0.118	0.363-0.876
Total	117	0.829	0.058	0.682-0.916	237	0.952	0.010	0.927-0.969	293	0.779	0.050	0.662-0.859
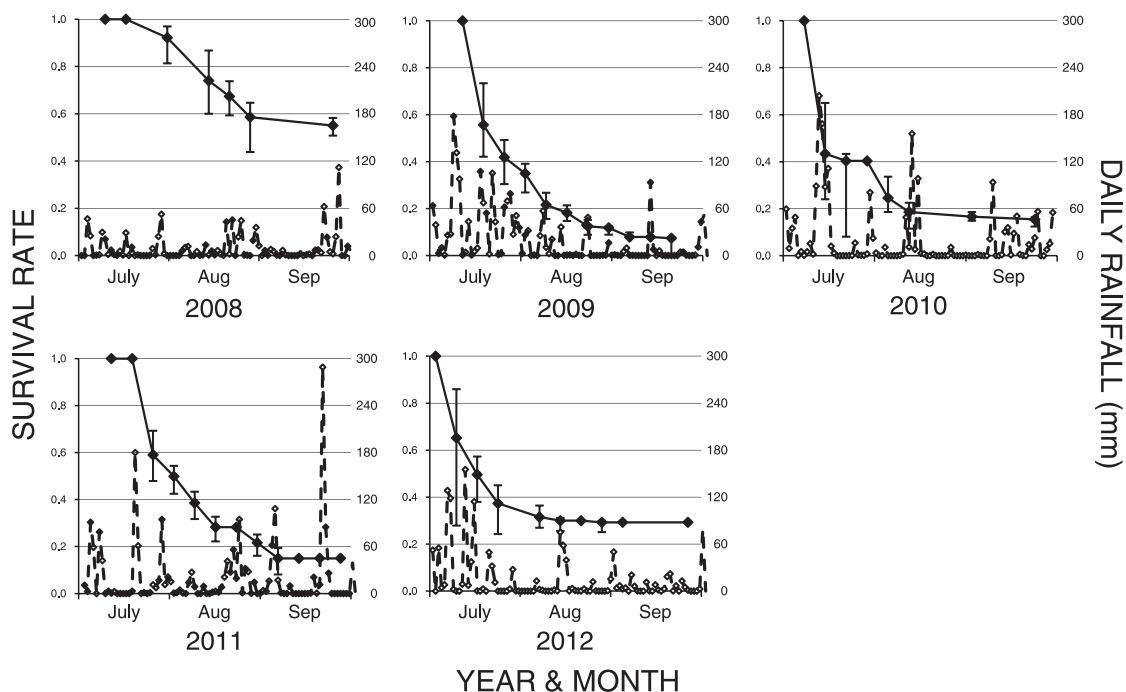
Figure 2. Relationship between weekly chick survival rate (◆) and daily rainfall (◇) during 2008-2012 on Mt. Norikura, Honshu, Japan. Error bars show 95% CI.

(412.2 mm and ± 105.9) due to a typhoon passing the area.

Discussion

The average clutch size of Japanese rock ptarmigan (5.7 eggs; see Table 1) was among the lowest reported clutch sizes for this species; i.e. 5.9 eggs in the Pyrenees (Novoa et al. 2011), 6.5 eggs in the French Alps (Novoa et al. 2011), 6.8 eggs in the Italian Alps (Scherini et al. 2003), 8.3 eggs on Attu Island, Alaska (Kaler et al. 2010), 8.7 eggs in Windy Lake, Canada (Cotter 1999), 10.9 eggs in Iceland (Magnússon 2005) and 7.5 eggs in Svalbard (Unander & Steen 1985). With the exception of the Svalbard population, variation in clutch size

of rock ptarmigan may be related to a latitudinal gradient.

In our study, clutch size was not different among years, which was different from the results of other studies in which clutch size was related to the timing of snowmelt and condition of females (Unander & Steen 1985, Watson et al 1998). To assess this relationship in Japanese rock ptarmigan, further sampling and a long-term study should focus on the relationship between environmental conditions (such as timing of snowmelt) and clutch size.

Our average nest success (0.733 ± 1.071; see Table 1) was similar to nest success reported previously for our population (Sawa et al. 2011) and for a nearby population at Mt. Tateyama located at a distance of 65 km from our study area (0.75; Toyama Rock Ptarmigan Research Group 2002). However, nest

Table 5. Weekly variation of weather data and correlations with chick survival of Japanese Rock Ptarmigan on Mt. Norikura, Honshu, Japan. The average weekly values for rain, weather index and temperature during each period are shown with ± SD; * P < 0.05, ** P < 0.01

Weeks after hatch	Weather condition			Correlation between weekly survival		
	Rain (in mm)	Weather index (0~63)	Temperature (°C)	Rain	Weather index	Temperature
1-2	195.2 ± 136.9	33.3 ± 9.9	11.3 ± 1.6	-0.855**	-0.691*	0.669 *
3-4	107.4 ± 89.7	30.8 ± 12.7	12.2 ± 0.9	-0.351	-0.432	0.334
5-6	73.8 ± 79.9	23.2 ± 11.0	12.6 ± 1.0	0.366	0.294	-0.161
7-11	93.1 ± 92.1	26.2 ± 10.8	10.6 ± 2.3	-0.151	-0.435	-0.112

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success of our study population was generally higher than other rock ptarmigan populations (i.e. 0.68 in the Pyrenees (Novoa et al. 2011) and 0.40 in the French Alps (Novoa et al. 2011), 0.50 in the Italian Alps (Scherini et al. 2003), 0.50 on Attu Island (Kaler et al. 2010), 0.55 for first clutch in Canada (Cotter 1999), 0.57 and 0.84 for first clutch in two populations on Iceland (Aðalsteinn 2012) and 0.44-0.48 on Svalbard (Unander & Steen 1985)).

Most nests failed because of predation caused by terrestrial mammals like red fox, marten and ermine. Mesocarnivores were also the main cause of nest loss on Svalbard (Unander & Steen 1985), in the French Alps, the Pyrenees (Novoa et al. 2011) and in the Italian Alps (Scherini et al. 2003). However, daily survival rate of nests, hatchability and female survival during June were relatively stable among years, which suggested that nest predation had relatively little influence on total reproductive success of our study population. All the nests we found were placed under creeping pine. Sawa et al. (2011) suggested that the reason of high nest success of Japanese rock ptarmigan was related to the dense nesting cover provided by creeping pine.

Chick survival was strongly correlated with variation in weather conditions, particularly rainfall, during the first two weeks of the brooding season. Other studies have suggested similar negative effects of weather on chick survival in ptarmigan (Garðarsson 1988, Scherini et al. 2003, Novoa et al. 2008, Kaler et al. 2010), but we showed that the negative effect of weather occurred during the first two weeks of the brooding season (see Fig. 2 and Table 5). Harsh weather can directly decrease chick vitality because of their inability to thermoregulate efficiently. Tetraonoid chicks must be brooded periodically by females during the first few days after hatching, particularly on rainy days (Theberge & West 1973, Erikstad & Spidsö 1982). Chicks of Japanese rock ptarmigan were brooded for over half of the day during the first week post hatching, even on days with no inclement weather (Omachi Alpine Museum 1992). Brooding time gradually decreased as chicks grew up, and was little seen after a month post hatching (Omachi Alpine Museum 1992). This latter observation supported our results in that there was little correlation between survival and weather after the third week post hatching.

Our population appeared to have lower chick survival than other populations of rock ptarmigan at the same stage. For example, in a Canadian population, survival to three weeks of age was 0.75 (Cotter

1999) vs our survival of 0.58, and at five or six weeks of age, it was 0.85 in Svalbard (our calculation from Unander & Steen 1985), 0.74 in Iceland (our calculation from Magnússon 2005) and 0.54 in the Italian Alps (our calculation from Scherini et al. 2003) vs our survival of 0.46.

Novoa et al. (2008) suggested that their study populations, which inhabited a southern mountain range in Europe, had higher rainfall and more unpredictable weather in the post-hatching period than did the arctic populations. The average total rainfall the month post hatching on Mt. Norikura was higher and more variable (650 ± 281 mm) than Novoa et al.'s (2008) population in the Pyrenees (66.5 ± 38.2 mm). These results suggested that Japanese populations may have been populations more susceptible to variation in weather conditions.

Management implications

Our results suggested that management activities which result in increased survivorship of chicks are important to Japanese rock ptarmigan viability, because the highest mortality and the greatest variation in chick survival occur during four weeks post hatching. We showed that inclement and unpredictable weather likely affected chick mortality, but predation was also a factor that influenced chick mortality (H. Nakamura & A. Kobayashi, unpubl. data). Thus, we recommend management activities which result in protection of chicks from increment weather and predators to increase chick survival such as protecting broods in cages placed within their habitat during the first four weeks of the brooding season. If a few broods can be protected until chick independence using this method, it may reduce or stop the local population decrease.

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