Reproductive Ecology of Three Tibetan Waterbird Species, with Special Reference to Life-History Alterations along Elevational Gradients

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Xin Lu (2011) Reproductive ecology of three Tibetan waterbird species, with special reference to life-history alterations along elevational gradients. *Zoological Studies* **50**(2): 192-202. Life-history theory predicts that birds nesting at higher elevations will have lower reproductive output due to ecological constraints. Higher-elevation birds should allocate more energy into individual offspring through producing fewer and larger eggs to allow their offspring to better survive the harsh environments. To test the prediction, I collected reproductive data on 3 waterbirds, the Mallard *Anas platyrhynchos*, Common Moorhen *Gallinula chlorpus* and Eurasian Coot *Fulica atra*, at Lhalu Wetland (3650 m in elevation), the largest marshland with macrophytes on the Tibetan Plateau. These birds became regular nesters after prohibition of yak grazing and reed harvesting in the wetland since 2003. Mallards laid eggs from mid-Apr. to mid-June, moorhens from early May to mid-June, and coots from mid-May to late June. Clutch size and egg size of these high-elevation waterbirds were smaller or intermediate compared to those of their lowland counterparts, partially supporting the prediction. The pattern might be associated with a balance between environmental harshness and allocation of body reserves in terms of the number of clutches produced annually, and the number and size of eggs within a clutch across elevational gradients. The high-elevation mallards and moorhens primarily used reeds *Phragmites australis* as nesting habitat (with 92% and 68% of nests located there, respectively), whereas coots preferred rushes *Juncus effusus* (77%). Predation by mammals and flooding contributed to about 1/2 of the failed mallard and moorhen nests, whereas predation was responsible for the majority of coot nest loss. My data also suggest the importance of wetland management based on species-specific habitat requirements for conserving this breeding waterbird assemblage. http://zoolstud.sinica.edu.tw/Journals/50.2/192.pdf

Key words: *Anas platyrhynchos*, *Fulica atra*, *Gallinula chlorpus*, High elevation, Life history.

Elevation is an environmental gradient along which organisms shift their life-history strategies. In birds, studies aiming to examine elevational variations in life-history traits focused on terrestrial, mountain-dwelling taxa with altricial young (Badyaev 1997, Badyaev and Ghalambor 2001, Lu 2005 2008, Zeng and Lu 2009, Lu et al. 2009 2010a b). Those studies found a general tendency that due to environmental harshness, higher-elevation birds begin breeding later, experience shorter breeding periods, make fewer nesting attempts per year, and produce smaller clutches and larger eggs. Hence, higher-elevation birds have a total lower annual reproductive output, but put more energy into individual offspring compared to their lowland counterparts.

However, few studies have examined this topic with respect to waterbirds except for a case study on the Canada Goose *Branta canadensis* (Dunn and MacInnes 1987), most likely because our ability to acquire demographic data on high-elevation waterbirds is limited. Waterbirds where young are precocial invest more in egg production in terms of clutch mass relative to body mass, and offspring fitness depends on the egg size more heavily than in passerines with altricial

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young (Alisauskas and Ankney 1992). Therefore, waterbirds breeding in higher-elevation habitats are expected to allocate their body reserves through a trade-off between egg size and clutch size.

The Mallard *Anas platyrhynchos*, Common Moorhen *Gallinula chlorpus*, and Eurasian Coot *Fulica atra* nest in a variety of lowland wetlands over Eurasia and northern America (Palmer 1976, Cramp 1977 1980), and also breed on the Tibetan Plateau, a highland where many species are at the upper limits of their breeding elevations (Zheng et al. 1983). These high-elevation species provide a unique opportunity to test the life-history strategies along elevational gradients among waterbirds. Herein, I report their reproductive data including the egg-laying season, clutch size, egg size, nesting success, and nest site selection collected from a Tibetan wetland located at 3650 m near Lhasa City. In particular, I focused on the clutch size and egg size, the two important life-history variables which have evolved in specific environments (Lack 1967, Christians 2002). I predict that Tibetan waterbirds have smaller clutches of larger eggs than conspecifics at lower elevations.

A quarter of the China's natural wetlands occur on the Tibetan Plateau (China Wetland 2010). Wetlands in this region are characterized by scarcity of emergent vegetation, especially at elevations above 4000 m (Löffler 1969, Scott 1989). Even at 3000-4000 m, emergents are scattered in small patches (most with an area of < 3 km^2, with an overall total of < 20 km^2; Zhao 1988, Wang 2003). Such vegetation is critically important for reproduction of some waterbird species. It was shown that populations at the extremes of a species' range may be of particular conservation value because of the small and variable population sizes and low genetic variability (Hardie and Hutchings 2010). Therefore, the 2nd objective of this study was to develop recommendations for conservation of these high-elevation waterbirds based on knowledge of their nest site characteristics and habitat requirements.

MATERIALS AND METHODS

Study area and species

I conducted the study at the Lhalu Wetland (29°40'N, 90°05'E), which is situated at 3650 m close to Lhasa City, Tibet. It has a total area of 6.2 km^2, with 30% being covered by emergent

vegetation, and 70% by meadow vegetation (with a height of < 30 cm). The emergent vegetation consists of the Common Reed *Phragmites communis*, Common Rush *Juncus effusus*, and Sweet Flag *Acorus calamus* (Li et al. 2008). In this high-elevation region, marshlands with macrophytes only occur below 3800 m with Lhalu being the largest one (Zhao 1988, Wang 2003). Native marshlands have declined by 40% since the 1950s due to human land use practices. To protect this wetland, a local nature reserve was established in 1995, and was listed as a national reserve in 2005. However, the wetland was subjected to heavy grazing by yaks and reed harvesting by local people until the fall of 2003, when a fence system was built and these human activities were largely restricted (Dunzhu 2008).

Mallards and coots are found in the Lhasa region year round. In winter, they are commonly seen in rivers (Lhasa and Yanglong Zangbu Rivers), lakes, reservoirs, and wetlands, being numerically abundant in rivers and relatively rare in the other wetland types. Moorhens are migratory, and observations of this species are rare throughout winter (Lang et al. 2007).

Field procedures

I systematically searched for nests through-out a 320-ha plot (encompassing 110 ha of emergent marshes and 210 ha of meadows) of the wetland during the 2001, 2002, 2004, and 2007 breeding seasons. On finding a nest, I marked it with numbered flag, described the nest-site characteristics (type and height of vegetation, water depth, and distance to the edge of the vegetation using a tape measure), and took measurements of the nest and its contents (egg mass using an electronic balance, and egg length and breadth using a caliper). Subsequent visits were made at least once per week to estimate the nest contents and monitor the nest fate. I visited the nests at 1-2 d intervals if they were in the laying stage or ready to hatch to determine when these events occurred. To reduce possible influences of observer activities on a nest's fate such as providing some cues to predators, I tried to restore the vegetation around the nest back to its former conditions after each nest inspection as much as was possible. Some nests were checked only 1 or 2 times during the breeding period, and the data from those were used to establish nest-site features of egg size or clutch size if possible.

The date on which incubation commenced

was determined if a female flashed from the nest, or the eggs were warm when I checked them. The incubation period was defined as the time from the laying of the last egg to the hatching of the last young. Daily weight loss of each egg was estimated through weighing it when the nest was regularly checked during the incubation period. For some nests with no eggs present, ready separation of the vitelline membrane from the shell provided evidence that eggs had hatched and had not been lost to predation. A nest was considered to have been destroyed by predators if the nest bowl contained broken egg fragments with remains of yolk on the ground. A nest was considered to have been abandoned if the hen was absent, the eggs were cold, and there was no evidence that she had returned again. Eggs that failed to hatch were always left in the nests. I opened the eggs to determine whether developing embryos were present. If not, I considered the egg to have been unfertilized. Conspecific brood parasitism is common in waterbirds (Yom-Tov 2001). The occurrence of a parasitism event was assumed if more than 1 egg was laid per day, or new eggs were added after clutch completion (Post and Seals 2000).

Data analyses

The clutch initiation date was determined by counting eggs (assuming 1 egg was laid per day) and estimating the stage of embryo development according to the relationship between the fresh egg mass and egg dimensions along with the daily mass-loss rate (Hoyt 1979, Zicus et al. 2004). Egg size was measured using an egg volume index (length × breadth^2). Nests were considered successful if there was evidence that at least 1 young had fledged. To account for the bias caused by potential differences in nesting failure across the breeding season, I estimated nesting success by Mayfield's (1975) method. Only nesting attempts with a known fate were used to calculate reproductive success. The sample size was too small to assess annual variations in reproductive performance in many cases. Because of an insufficient number of nests per year, I pooled data from different breeding seasons unless otherwise noted.

Chi-squared tests were performed to compare differences in nest site selection among vegetation types. Vegetation heights around the nest sites were compared among waterbird species using a one-way analysis of variance (ANOVA) with Fisher's least significant difference (LSD) post-hoc multiple tests used to examine the difference between 2 species. Relationships of clutch initiation date vs. clutch size, clutch size vs. egg size, and egg size vs. elevation were assessed by Spearman correlation coefficients. Probabilities were 2-tailed, and the significance level was set to $\alpha = 0.05$. Values are given as the mean ± standard deviation (SD).

RESULTS

Population dynamics

Prior to 2003, few waterbird nests were found in the Lhalu Wetland except for 2 mallard nests located in 2002 (Table 1). Moorhens appeared in the wetland as breeders in 2004, consistent with the time of prohibition of yak grazing (counts of the summer livestock over the 6.2 km^2 wetland included 1200 yaks and 180 horses in 2001 and 40 yaks and 2 horses in 2007), reed harvesting, and trespassing by local people due to establishment of a fence system surrounding the wetland in Aug. 2003. In 2007, coots were found

Table 1. Numbers of nests located for 3 waterbirds at Lhalu Wetland, near Lhasa, Tibet, during 4 breeding seasons. The investigation was conducted over a 320-ha plot (containing emergent marshes and meadows) for mallards and 110 ha (only marshes) for moorhens and coots

Year	Nest search effort (d)[a]	Number of nests		
		Mallard	Moorhen	Coot
2001	6	0	0	0
2002	6	2	0	0
2004	13	19	11	0
2007	12	25	9	13

[a]The number of days during which the entire wetland was investigated.

nesting there for the 1st time.

Breeding season

The egg-laying period of mallards lasted for 2 mo, beginning in the 2nd wk of Apr., and ending by the 2nd wk of June. The 2 other species laid eggs for 1.5 mo from early to mid-May until mid- to late June, (Fig. 1).

Nest-site selection

All 3 waterbird species used emergent vegetation (97.5% of 79 nests) more often than meadow (2.5% of 79 nests, Chi-squared test, $\chi_1^2 = 57.24$, $p < 0.001$). No nests were found in sweet flag. As to the vegetation used, nesting mallards favored reeds over rushes ($\chi_1^2 = 5.96$, $p = 0.02$), while coots exhibited an opposite preference ($\chi_1^2 = 18.07$, $p < 0.001$; Table 2). Moorhen nests were built in proportion to the availability of reeds and rushes ($\chi_1^2 = 0.01$, $p = 0.92$).

All 3 species nested in vegetation of similar heights (one-way ANOVA, $F_{2,40} = 0.26$, $p = 0.77$; Table 3). Mallards tended to nest in shallower water than did moorhens and coots ($F_{2,40} = 2.99$, $p = 0.06$; LSD post hoc, $p = 0.03$ and 0.09). This species also built their nests relatively far from the edge of emergent vegetation ($F_{2,40} = 7.68$, $p = 0.002$). More mallard nests were located on the ground (on small-meadow islands within reeds, 71.7% of 46 nests) than over water (28.3%). Nests of moorhens and coots all were cylindrical and over water. There were a few unused nests (1-3) within 20 m of some moorhen (4 of 20 nests) or coot nests (3 of 13 nests). Nests consisted of plant material that had obviously been collected from the immediate vicinity.

Systematic searches for waterbird nests throughout the emergent vegetation and potentially suitable meadow allowed me to calculate nest densities by dividing the number of nests located by the area of the study plot (320 ha for mallards and 110 ha for both moorhens and coots). The respective maximum densities were 0.08, 0.10, and 0.12 nests/ha for mallards, moorhens, and coots.

Egg size

Mallard eggs, which were elliptical and dark-white with no spots, had an average length of 54.5 ± 2.3 (range, 45.0-62.1) mm ($n = 148$) and width of 39.4 ± 1.2 (range, 35.0-41.8) mm. Eggs found during the laying period weighed 46.4 ± 1.8 (range, 43.4-49.0) g ($n = 19$). One egg within a 9-egg clutch was exceptionally small (32.9×27.1 mm). Moorhen eggs were dark-white with scattered brown markings, and measured 41.3 ± 1.6 (range, 37.9-45.0) mm ($n = 68$) long and 29.5 ± 1.0 (range, 27.0-32.1) mm wide, and weighed 20.4 ± 1.8 (range, 17.1-22.8) g, ($n = 15$ eggs prior to incubation). Coots produced dark-white eggs with brown spots distributed over the entire egg surface. The fresh mass was 35.0 ± 0.7 (range, 34.1-36.0) g ($n = 7$), and they were 51.7 ± 2.0 (range, 48.0-57.8) mm ($n = 37$) long and 36.0 ± 0.8
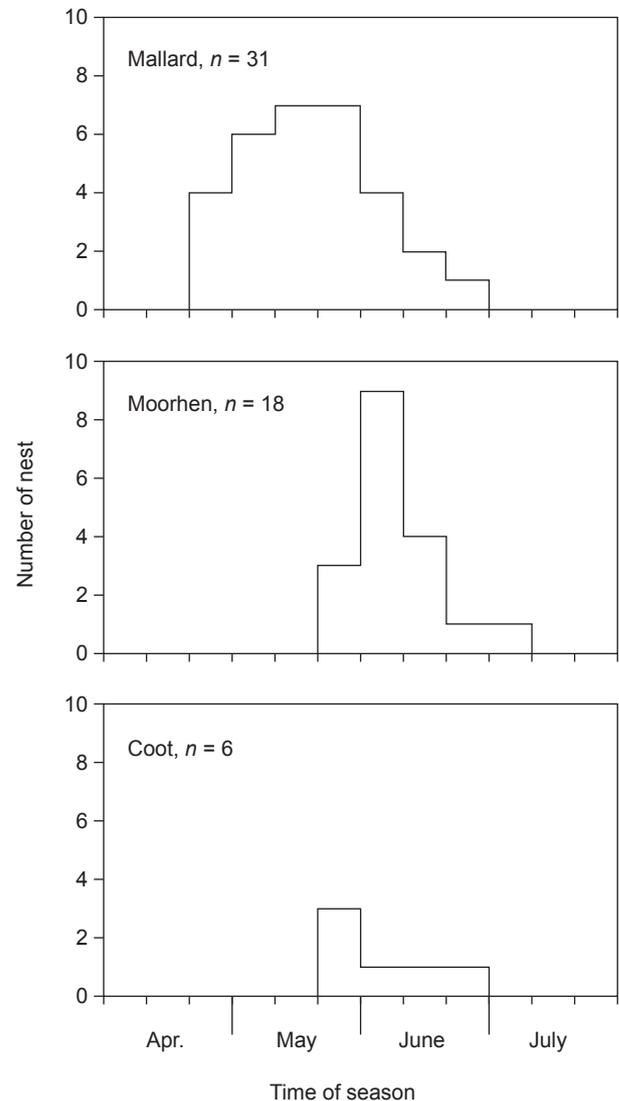

Fig. 1. Temporal distribution of the 1st egg dates for 3 waterbirds at Lhalu Wetland, near Lhasa, Tibet. The time of clutch initiation was arranged in 10-d periods, and data from different years were pooled.

(range, 34.5-37.9) mm wide.

Clutch size

The average size of clutches produced by mallards was 6.07 ± 1.62 (range, 4-9) eggs (n = 26). Coots had clutches of 5.00 ± 0.89 (range, 4-6) eggs (n = 6). There was no evidence that more than 1 egg was laid per day, or that new eggs were added after clutch completion for these 2 species. The clutch size of moorhens was 7.94 ± 1.14 (range, 6-10) eggs (n = 17). There was a cutch (with a final clutch size of 7 eggs) in which 2 additional eggs appeared several days later than all of the other eggs, presumably the result of conspecific brood parasitism. After excluding the 2 eggs from the analysis, the average clutch size was 7.82 ± 1.13 eggs (n = 17).

There was no significant relationship between the clutch initiation date and clutch size for any species (mallard, r_s = -0.28, n = 21, p = 0.21; moorhen, r_s = 0.004, n = 17, p = 0.99; coot, r_s = -0.21, n = 5, p = 0.73). The average volume of eggs within a clutch had a marginally significant negative correlation with the size of the clutch in coots (r_s = -0.80, n = 6, p = 0.055). In the other species, this relationship was lacking (mallard, r_s = 0.22, n = 21, p = 0.33; moorhen, r_s = -0.15, n = 14, p = 0.60).

Incubation

Female mallards began incubation before finishing a clutch (with the 3rd and 4th egg in a 6- and 7-egg clutch, respectively). Hatching of a nest of 8 eggs lasted 2 d. In moorhens, the time at which incubation began varied; before laying of the 6th egg in 3 nests, after the 3rd egg in 1 nest, and with clutch completion in another. The hatching interval differed between the 1st and last eggs in a clutch, at within 2 d in 2 nests, at least 3 or 6-7 d in 3 different nests. For mallards, incubation lasted 25, 29, and 34 d for 3 clutches, and more than 22 d for 2 others. It was 20 d in 1 moorhen nest and 22 d in the other. The incubation period for coots was not determined.

During incubation, egg weights declined. Daily rates of weight loss were estimated to be 0.29 ± 0.11 (range, 0.1-0.5) g/d (27 repeated measurements of 17 eggs from 3 nests) in mallards, 0.19 ± 0.07 (range, 0.03-0.3) g/d (107 measurements of 72 eggs from 10 clutches) in moorhens, and 0.23 ± 0.13 (range, 0-0.63) g/d (32 measurements of 15 eggs from 3 nests) in coots.

Breeding success

The proportions of nests from which at least 1 chick fledged were 44.7%, 68.8%, and 42.9%

Table 2. Nest site selection with respect to types of vegetation by 3 waterbirds at Lhalu Wetland, near Lhasa, Tibet

Vegetation type[a]	Proportion of the wetland (%)	Number of nests		
		Mallard	Moorhen	Coot
Reeds	33.8	41	16	3
Rushes	9.0	2	4	10
Sweet flag	2.0	0	0	0
Meadow	55.2	3	0	0

[a]Details are provided in the text.

Table 3. A summary (mean ± standard deviation, range) of the height of the vegetation, water depth around the nest, and distance to the edge of the emergent vegetation for 3 waterbirds at Lhalu Wetland, near Lhasa, Tibet

Environmental variable	Mallard (n = 20)	Moorhen (n = 14)	Coot (n = 9)
Vegetation height (cm)	127 ± 34, 67-180	126 ± 24, 80-160	119 ± 23, 80-155
Water depth (cm)	16 ± 9, 0-30	23 ± 9, 4-36	22 ± 11, 6-35
Distance to vegetation edge (m)	14 ± 8, 5-30	7 ± 4, 3-15	7 ± 3, 2-12

for mallards, moorhens, and coots; the chances that a nest would fledge at least 1 young, which were estimated by Mayfield's (1975) method, were 17.1%, 43.6%, and 14.9%, respectively (Table 4). Among 17 successful mallard nests, 10 had a few (1.9 ± 0.9; range, 1-4) eggs that failed to hatch. Of the 19 eggs, 2 were unfertilized. There were 3 unhatched eggs in a 9-egg moorhen nest, two of which were had been added after clutch completion. All eggs in 3 successful coot nests hatched. Complete nesting failure in mallards and moorhen was attributed to nest abandonment (52.4% and 40.0%) and predation (42.9% and 40.0%, respectively). For coots, the majority of failed attempts were attributed to predation (92.9%).

DISCUSSION

Clutch size and egg size

Two of the 3 Tibetan waterbird species produced smaller and 1 intermediate-sized clutches compared to lower-elevation conspecifics (Table 5). A latitudinal increase in clutch size is a general rule exhibited by many passerines (Lack 1954), but the tendency seems to be opposite for waterbirds (Owen 1980, Dunn and MacInnes 1987, but see Rubolini and Fasola 2008). A further reduction in clutch size may thus be expected if taking the latitude that is relatively low at my study site into account. Dunn and MacInnes (1987) who work on the Canada Goose also reported a slight

decline in clutch size when elevations increased from 10 to 2000 m. In comparison with their lowland counterparts, high-elevation mallards laid smaller eggs (r_s = -0.98, n = 6, p = 0.008), whereas 2 other Tibetan waterbird species had eggs of an intermediate size.

When facing energy constraints, birds may allocate their body reserves through trade-offs between clutch size and egg size. Selection at high elevations should favor large eggs in small clutches, because large eggs have the advantages of reduced thermoregulatory costs and increased survival of the resulting young (reviewed in Johnson et al. 2006). However, the above comparisons suggest that high-elevation waterbirds produce fewer eggs, but the eggs were smaller or at least no larger than their low-elevation counterparts. The latter case differs from the pattern followed by some Tibetan passerines (Lu 2005 2008).

Energy constraints on egg production (Lack 1967 1968, Arnold and Rohwer 1991) and incubation/brood rearing (Charnov and Krebs 1974) are 2 common hypotheses to explain the evolution of clutch size among precocial species. Both hypotheses predict that birds suffering from food shortage before laying will have a lower annual reproductive output because they cannot accumulate sufficient body reserves for egg formation, incubating eggs, or rearing a brood. Meanwhile, evidence showed that females breeding in environments with limited local food resources lay small eggs, because such eggs are less energetically demanding (Eldridge and Krapu

Table 4. Reproductive success (estimated by the proportion of successful nests using Mayfield's method) and causes of nesting failure of 3 waterbirds at Lhalu Wetland, near Lhasa, Tibet

	Mallard	Moorhen	Coot
Proportion of successful nests			
No. of nests observed	38	16	7
No. of successful nests	17	11	3
Percent (%) success	44.7	68.8	42.9
Mayfield's method			
Total exposure days	471	177	63
Nesting period (d)	36	29	29
Percent (%) nest survival probability	19.4	43.6	14.9
No. of failed nests	21	5	4
Deserted	11	2	1
Predated	9	2	13
Disappeared	1	1	0

1988, Stevenson and Bryant 2000, reviewed by Christians 2002). In high-elevation environments, food availability for these waterbirds may be limited for the following reasons: (1) comparatively low primary productivity of highland wetlands (Zhou et al. 2004) and poor invertebrate richness (Jiang et al. 1983, Wang et al. 1992); (2) a relatively short photoperiod at mid-latitudes, which can also limit a female's ability to extensively forage; and (3) low oxygen content, which may restrict the ability of animals to metabolically process body materials for reproductive output (reviewed in Dillon et al. 2006). These ecological constraints may be strong enough to limit the production of eggs in terms of both egg number and egg size. The absence of a correlation of clutch size and egg size with elevation was also observed in a few passerines nesting on the Tibetan Plateau (Lu et al. 2009, Lu unpubl. data).

Clutch initiation dates (mid-Apr.) by high-elevation mallards were similar to or slightly later than those of their lowland counterparts (Finland, mid-Apr. Hildén, 1964; Louisiana, USA early Apr.; California, USA late Feb., Nancy et al. 2010). Lhasa moorhens began laying later (early May and mid-May) than those in East China (early Apr., pers. data), and southern England (late Mar., Huxley and Wood 1976; North America, early Apr. to early May, Bannor and Erik et al. 2010).

Coots initiated breeding in mid-May at my study site, later than most European populations (early Apr., Cramp 1977) and an Algerian population (early or mid-Mar., Samraoui and Samraoui 2007). Breeding times in both Rallidae species lasted only 1.5 mo, shorter than those of their low-elevation counterparts (2-4 mo). Research on lowland mallards revealed that birds raise only 1 nest per year, but often renest if the 1st clutch is destroyed (Bellrose 1980). Moorhens and coots are a facultative double-brooding species, but those nesting in northern regions rarely produce a 2nd brood (Post and Seals 2000, Brisbin and Mowbray 2002). The compressed breeding window makes it less likely that high-elevations waterbirds will hatch more than 1 clutch during a breeding period. Hence, energy constraints on high-elevation waterbirds that raise a single brood during the breeding season are expected to be relatively less heavy. This may explain the intermediate-sized clutches or eggs produced by moorhens and coots.

Other nesting parameters

The maximum densities in Lhalu were 0.08, 0.10, and 0.12 nests/ha for mallards, moorhens, and coots, respectively. The figures are relatively low compared to their counterparts breeding in

Table 5. Comparisons of the mean clutch size (range) and egg size of 3 Lhasa waterbirds with those of their lowland counterparts

Species	Location	Latitude (°N)	Elevation (m)	Clutch size	Egg volume (cm³)	Source
Mallard						
	S. Tibet	29	3650	6.1 (4-9)	85.5	This study
	Finland	60	0	8.2 (6-11)	95.8	Hildén 1964
	California	38	5	8.6	100.0	Ackerman and Eadie 2003
	Minnesota	46	< 200	10.3	95.8	Zicus et al. 2004
	Dakotas	48	< 200	10.4 (7-13)	95.4	Duebbert et al. 1983
	N. India	34	1584	8.3 (4-13)	92.8	Shah et al. 2009
Moorhen						
	S. Tibet	29	3650	7.8 (6-10)	35.9	This study
	N. China	37	790	8.3 (5-12)	32.3	Liu et al. 1985
	N. China	39	820	8.7 (5-12)	34.4	Su and Liu 1997
	the UK	52	100	6.6 (2-13)	41.3	Huxley and Wood 1976
	USA	40-50	< 1000	7.0	42.3	Nancy et al. 2010
Coot						
	S. Tibet	29	3650	5.0 (4-6)	67.2	This study
	N. China	41	1019	8.0 (5-12)	68.7	Xing and Yang 1989
	N. China	47	140	8.0 (8-12)	65.0	Wang et al. 1990
	N. Algeria	36	843	6.1 (1-11)	70.4	Samraoui and Samraoui 2007
	Palearctic	40-60	< 200	6.5-8.8	-	Cramp 1980

low-elevation mainland wetlands (mallards, 2.0 nests/ha in Buckinghamshire, UK, Hill 1984; 0.2-0.3 nests/ha in North Dakota, USA, Kruse and Bonnie 1996; moorhens, 0.9 nests/ha in South Carolina, USA, Post and Seals 1991; 1.0 nests/ha in the Netherlands, Brinkhof et al. 1993; coots, 1.5 nests/ha in southern Lithuania, Stanevičius and Švažas 2005; 2.5 nests/ha in Algeria, Samraoui and Samraoui 2007). There is a general rule for a decreasing abundance of species at the margins of their distributions along environmental gradients due to resource depletion, physical stress, and competitive exclusion (Brussard 1984).

A seasonal decline in clutch size commonly occurs in single-brooded birds, including mallards (Hill 1984, Lokemoen et al. 1990) and coots (Brinkhof et al. 1993, Samraoui and Samraoui 2007). This pattern probably occurs because early breeders are older and more experienced and are thus able to find suitable nest sites and produce larger clutches (Hochachka 1990). However, the trend was not evident in the high-elevation populations. A likely reason is that a recently established population in a wetland may have a relatively even age structure, especially if the birds that discover the wetland are young, as they tend to be more exploratory especially during their 1st year. These birds have to take some time to accumulate local knowledge and experience required to successfully breed.

Conspecific brood parasitism is widespread among waterfowl, typically including mallards, moorhens, and coots (Yom-Tov 2001). In this study, I only found 1 example in moorhens (11% of 9 monitored nests). In contrast, the proportions of nests parasitized were 15% in a population in England (McRae 1995) and up to 40% in 2 other *Fulica* species (Lyon 1993, Jamieson et al. 2000). It remains unclear of the adaptive aspects of the elevational difference in the parasitism rate.

Due to the diffusion of water vapor from an egg's interior through the eggshell, bird eggs lose about 15% of their initial mass during incubation (Ar and Rahn 1980). Daily mass losses estimated from Rahn and Ar's (1974) model ($M_{H2O} = 0.015W^{0.74}$, where W is the fresh egg mass) were 0.2566, 0.1369, and 0.2084 g for mallards, moorhens, and coots, respectively, lower than values I observed (0.2852, 0.1945, and 0.2280 g). This supports the idea that the rates of daily water loss should increase when birds nest at high elevations since the diffusion coefficient for gases is inversely related to the barometric pressure (Carey 2002).

Nesting success of mallards in the study area (45%), measured by the proportion of nests from which at least 1 young fledged, was within the normal range reported for this species in other comparable lowland marshes where waterfowl are under protection (43% in the UK, Hill 1984; 44%-66 % in North America, Krapu et al. 1979, Arnold et al. 1993; 68% in Latvia, Laubergs and Viksne 2004). This is above the threshold level (15%-20%) necessary to sustain a population (Cowardin et al. 1985, Klett et al. 1988). Moorhens in Lhasa had a 69% nesting success rate, similar to 63% in Louisiana, USA (Helm et al. 1987) and 55%-80% in North America (Bannor and Erik 2010). Of the coot nests, 43% were successful compared to 34%-49% for this species breeding in different areas of the western Palearctic (summarized by Cramp 1980). Predation on average accounts for 80% of nest losses in birds (Martin 1993), which is particularly true for ground nesters like some waterbirds. However, for mallards and moorhens in the Lhasa area, nest predation rates (40%-43%) were relatively low. This may be explained by the absence of gulls, crows, and snakes (the main predators of breeding waterbirds; Hill 1984, Samraoui and Samraoui 2007, Bannor and Erik 2010, Nancy et al. 2010), along with good nest concealment from avian predators (the Magpie *Pica pica* and the Grey-backed Shrike *Lanius tephronotus*; Hill 1984) in the dense cover and inaccessibility to terrestrial mammalian carnivores (the Mountain Weasel *Mustela altaica* and the Tibetan Fox *Vulpes ferrilata*; Cramp 1977 1980, Arnold et al. 1993). The large contribution of predation to coot nest failure, as reported in May and June 2007, might have been related to reduced water levels, which exposed their nests to terrestrial predators such as weasels and foxes. Nest desertion was more likely to be a result of increased water levels due to an influx of water into the wetland by human interventions.

Implications for conservation

My results suggest that wetland protection by restricting the cutting of emergent vegetation and grazing by large herbivores might result in attracting breeding waterbirds in a very short period of time. A similar pattern was observed in a northern US wetland (Kruse and Bonnie 1996). Coots returned to the wetland as nesters about 1-2 yr later than 2 other species, perhaps because the rush community, their favored nesting habitat,

had not become reestablished until 2007 (pers. obs.).

Nest site selection differed among the 3 species. Nesting mallards and moorhens preferred reed patches, whereas rush patches were attractive to coots. No nests were found in sweet flag, perhaps because the vegetation is too dense for birds to move around in it. Mallards tended to nest in uplands, and the 2 other species nested in plant patches over water. In this highland wetland, mallards began to breed earlier in the season than did the other waterfowl and required taller reeds to shelter their nests than they do in other regions (Hill 1984). In addition, mallards built nests farther from the edge of the emergent vegetation, more likely as a result of the ducks selecting larger sizes of reed patches in which to nest. Therefore, vegetation and water management which take nesting habitat requirements of different species into account will be important for supporting a stable breeding waterbird assemblage.

At present, the Lhalu Wetland suffers from a shortage of water because the river that supports it has been experiencing a decline in flows (Dunzhu 2008). Wetland managers have to use water from the Lhasa River which is connected by a ditch to sustain the wetland. The current management practices do not take waterbird breeding requirements into account. For example, no water was supplied during the severe drought in May and June 2007, so that a number of fish and aquatic invertebrates died, and waterfowl had to aggregate in small surviving pools (< 100 m^2) to forage for a few weeks. However, subsequent water influx caused a rapid rise in the water level (up to 80 cm), leading to the failure of some waterbird nests due to flooding. This further highlights the importance of scientific management of this wetland.

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Three species, Fagus sylvatica, Picea abies and Pinus sylvestris, showed an opposite pattern while for other three species, such as Quercus ilex, Acer pseudoplatanus and Q. petraea, we were no able to detect changes in distribution. These findings are in contrast with theoretical predictions and show that tree responses to climate change are complex and are obscured not only by other environmental factors but also by internal processes related to ontogeny and demography. Download full-text PDF. Source. Â Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? Bodin et al. Journal of Vegetation Science 2013. Ecology of sprouting in woody plants: the persistence niche Bond et al. Trends in ecology & evolution 2001. History of Research on Elevational Species Richness . Patterns in Species Richness with Elevation . Methodological Issues . Â Elevational Gradients in Species Richness. Table 1 Continued Biotic interactions Species distributional interactions. Evolutionary history Diversity highest in areas of high speciation and/or low extinction. # Species. # Species of Competitors. Â The metabolic theory of ecology (MTE) is the theory that most directly connects diversity and temperature, and uses the bio-chemical kinetics of metabolism to predict changes in diversity of ectotherms along temperature gradients by linking ecological and evolutionary processes to an organism's metabolic rate (Brown et al., 2004). Life history theory is an analytical framework designed to study the diversity of life history strategies used by different organisms throughout the world, as well as the causes and results of the variation in their life cycles. It is a theory of biological evolution that seeks to explain aspects of organisms' anatomy and behavior by reference to the way that their life histories—including their reproductive development and behaviors, post-reproductive behaviors, and lifespan (length of time alive)