River bed restoration boosts habitat mosaics and the demography of two rare non-aquatic vertebrates

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A R T I C L E   I N F O
Article history:
Received 24 December 2010
Received in revised form 26 April 2011
Accepted 2 May 2011
Available online 26 May 2011

Keywords:
River ecosystem dynamics
Gravel exploitation
Bird conservation
Closed-population estimation
Probability of detection
Actitis hypoleucus
Charadrius dubius
WinBUGS

A B S T R A C T

Many river revitalization projects are currently under development, but we still lack proper assessments of their effects on biodiversity, especially regarding non-aquatic vertebrates. We analysed the progressive changes in habitat mosaics, and the demographic response of two rare species of wading birds along a Swiss section of the Rhone river over a period of three decades. During the period preceding revitalization, the diversity of the habitat mosaic had been steadily declining. This impoverishment could however be reverted after 1994, when the revitalization was initiated: in 2006, the re-established habitat matrix was more diverse than at any time during the previous 27 years. The formerly channelized stream underwent radical transformation as it mutated into a heterogeneous braided river boosting pioneer riverine habitats. This has led the two wading bird species to establish significantly more territories than before. Population size of Actitis hypoleucus and Charadrius dubius increased by 83% and 20%, respectively, between 1995 and 2007. During the same period, A. hypoleucus declined dramatically in Switzerland as a whole, whilst C. dubius showed no distinct population trend. The response of the two waders may have resulted from an increase in the number of lateral arms of the river, where the availability of productive temporary ponds provides excellent foraging opportunities. A significant proportion of these habitats was created by a targeted extraction of sediments with the objective to promote biodiversity while maintaining economic activity and improving security against floods. This suggests that gravel exploitation is not incompatible with efficient river restoration.

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1. Introduction

Rivers are among the richest but also the most endangered ecosystems worldwide (Tockner and Stanford, 2002; Ward et al., 1999), with a species extinction rate five times greater than in terrestrial ecosystems (Bernhardt et al., 2005). This is because human activities mostly concentrate on plains and are often located close to rivers and their tributaries, thus exerting a huge pressure on riverine and riparian ecosystems. Due to this proximity to human activities and the inherent risks for the society and economy which arise from river dynamics – essentially floods and erosion – rivers have been radically modified over the past centuries (Jensen et al., 2006). The regulation of river dynamics was obtained first through the progressive, systematic rectification of river beds, essentially via the construction of levees and embankments for constraining water flow. Containments have profoundly altered water regimes and, in turn, habitat dynamics, dramatically modifying conditions for aquatic and terrestrial wildlife. The construction of levees and dikes has furthermore provoked a disconnect between the river bed and the surrounding habitats (permanent and temporary wetlands, riparian woodland, extensive agriculture, groundwater table), with the consequent loss of habitat connectivity and complementarity formerly present in the dynamic landscape mosaic (Pedrol et al., 2002). The practice of damming to regulate water flow has in turn markedly modified seasonal discharge regimes, resulting in a cascade of consequences on river dynamics and riverine ecosystems. As a result, biodiversity typical of running waters has vanished, for instance all species of plants and animals that occur only in the early stages of the vegetation succession following a flood (Allan and Flecker, 1993). In addition, the artificial regimes of discharge imposed by hydroelectric power plants have inflated the problem where dams have been erected primarily for electricity production (Vinson, 2001). All in all these severe...
changes in river dynamics have caused a drastic disruption of ecological processes and led to a major impoverishment of riverine and riparian habitats, i.e. aquatic and terrestrial biodiversity. Today, 90% of floodplains in Europe and North America have been reclaimed and their rivers constrained into channels which are functionally dead in ecological terms (Tockner and Stanford, 2002). In Switzerland, 95% of rivers have been converted from their pristine, natural state into rigid channels, thereby turning them into mostly monotonous ecosystems. This is a major conservation issue given that rivers harbour a large proportion of the indigenous biodiversity.

Restoring the integrity of river ecosystems should be the ultimate goal of any river rehabilitation project (Poudseigne et al., 2002; Tockner and Schiemer, 1997). This ideally necessitates reinstating river dynamics and connectivity functions with the nearby complementary habitats which characterize flood plains, such as wetlands and riparian forests, as well as extensive farmland (Rohde et al., 2005; Ward, 1998). In most parts of the developed world, the modern landscape with its intensive land-use through agriculture, industrial estates and human settlements rarely leaves room for integral river rehabilitation. Albeit we cannot restore wide flood plains, a few attempts towards more natural river dynamics have recently been made (Buijse et al., 2002; Rohde et al., 2004, 2005). One example is the renaturing project of the river Rhone in Finges, Valais, Switzerland. There, during the course of the 20th century the river bed was progressively channelled through the construction of levees. More recently, however, a succession of major floods led to the broadening of the river, as sections of the lateral levees were successively swept away by the strong currents and not subsequently replaced. In addition to the natural modification in the riverine habitats resulting from the reinstated river dynamics, human intervention further helped accelerate habitat restoration by the application of targeted gravel extraction to mimick natural habitat mosaics while avoiding excessive accumulation of sediments. This exploitation was clearly motivated by a biodiversity restoration objective but was designed so as to accommodate sustained, but re-oriented economic activities while abiding by safety rules and regulations (Oggeri, 2003, 2007). This paper documents the temporal changes operated in the riverine vegetation and habitat mosaic as well as the response of two threatened wading bird species following habitat improvements. It represents to our knowledge one of the first published assessments of the effects of river renaturation on non-aquatic vertebrates typical of riverine ecosystems.

2. Material and methods

The study was carried out between 1978 and 2007 along a section of the river Rhone at Finges (French names) in Valais, southwestern Swiss Alps (46°18′N 07°35′E; 535–610 m a.s.l.). The Rhone is the sole, longest section (8.8 km) of the plain upstream of the Lake Geneva, where the river has not been systematically channelized between levees. This is largely due to a steeper gradient in that section (0.9%) compared to other sections up- or down-stream (0.2%), and to the presence of a huge, steep and unstable dolomitic slope whose high rate of erosion – between 50 and 250 thousand m² sediments flowing into the Rhone every year – has led to the formation of an alluvial fan in the south-east of Finges. The combination of these features, coupled with three major floods in 1987, 1993 and 2000, recreated a braided, dynamic stream (Fig. 1). Upstream of Finges, a dam collects the river water which is then channelled underground to a hydro-electric power plant situated at the western end of the area. The dam collects up to 60 m³/s; this represents only 20% of the high waters in summer. In winter (October–March), however, the regime is massively affected, with only 3.5 m³/s remaining in the river bed, the minimum residual discharge required by Swiss legislation. The situation is a bit better in April (4 m³/s) and May (5 m³/s). The presence of gravelly soils renders the area difficult to cultivate, and so beyond the river sediments most of the land is covered by pine and riparian forests, although agricultural land is also present in places. Because of its particular natural features and biodiversity, the area has obtained the provisory status of Nature Park.

Our first task was to map habitat changes over time, based on a series of aerial photographs (Schmitz et al., 2009) taken in 1981, 1986, 1992, 1998 and 2006. We distinguished six major habitat types within the 370 ha wide study area situated in the core of Finges: (1) water and bare alluvial deposits (this category corresponds to the regularly submerged river channel sections; because water flow regimes fluctuate so much in these areas, even within a day, water and bare alluvial deposits were for all years merged into one group, irrespectively of observable water levels); (2) natural and artificial sand arms, which include temporary ponds; (3) alluvial deposits with 10–50% grass–bush cover; (4) alluvial deposits with 50–70% bush–small trees cover; (5) young riparian forest (>70% cover); and (6) others (farmland, pine forests, poplar plantations, steppe, gravel exploitation infrastructure, levees and houses). Habitats were delineated visually from the aerial photographs and digitized with GIS (MapInfo) on a 1:5'000 scale photogrammetric layer to estimate their respective surface areas. Particular interest was given to the temporal trends of habitats 2–4, which constitute the typical breeding grounds of two rare wading birds of Switzerland, which have each fewer than 100 breeding pairs (Schmid et al., 1998). Note that this stretch of the Rhone does not harbour typical waterfowl such as ducks and coots because of a torrential flow regime (Valais harbours the highest peaks in the Alps). The common sandpiper (Actitis hypoleucos) typically occurs in habitats 2–4, with a preference for 3 followed by 4. The little ringed plover (Charadrius dubius) inhabits habitats 2 and 3, with a preference for 2. We were also interested in changes in the habitat mosaic over time. We thus measured yearly habitat heterogeneity using Simpson’s index:

\[1 - D = 1 - \sum \frac{p_i^2}{C_0}\]

where \(1 - D\) = Simpson’s index of diversity, \(p_i\) = proportion of habitat category \(i\).

The two bird species were surveyed in May–June 1978, 1987, 1990, 1995, 1999 and 2007. The surveys consisted of standard walking transects along both sides of the river bed, from which all bird observations were mapped. Bird breeding behaviour was coded according to the best practice applied for international ornithological atlases (Sharrock, 1973). Only observations typically indicating a probable or confirmed breeding were retained (atlas code \(≥4\), Schmid et al., 1998); hence, late migrants and un-paired floaters were not considered. The approximate location of a given territory was estimated through simultaneously observing several neighbouring territory holders during the early season surveys, with subsequent observations being attributed to one previously located territory. The number of territories is thus reliable, whereas their precise location remains somehow more subjective. Similar methods applying the same criteria have been used in previous surveys of the two species (Parrinder, 1989; Valden and Holland, 1993; D’Amico, 2002). The survey effort varied between years: only one survey was carried out in 1987 and 1990, while three surveys were undertaken in 1999, four in 1995 and 2007, and five in 1978 (although detailed data proved to be unretrievable for this dataset). A typical transect survey lasted 15 h and took
place over two mornings. For the surveys made in 1995, 1999 and 2007, we fitted a closed-population capture–recapture model to estimate population sizes of both species. We adopted a logit-normal heterogeneity model (Coul and Agresti, 1999; Dorazio and Royle, 2003; Royle and Dorazio, 2008) implemented in a Bayesian framework using the WinBUGS software (Kéry, 2010; Lunn et al., 2000). For each species and year (1995, 1999 and 2007) respectively, our model made the following assumptions: (1) there is a constant number of $N$ territories available for detection during the three or four surveys in a year (the closed population assumption); (2) each territory has its own, constant detection probability and the distribution of logit-transformed, territory-specific detection probabilities is normal. There are no seasonal or other effects on detection probability apart from the so-called individual heterogeneity. This “heterogeneity model” is one of the standard models used for abundance estimation (Williams et al., 2002). However, its parameters can be very hard to estimate with such small sample sizes as ours. Therefore, we exploited one major asset of Bayesian inference, namely that external information can be formally combined with the information contained in a data set at hand, i.e. we used slightly informative priors in our analysis. Specifically, we made the additional assumption that there were at most 20 undetected territories for either species in 1995, 1999 and 2007, but that any value between 0 and 20 undetected territories was equally likely. With between 8 and 21 territories actually detected, this assumption appeared very plausible. Furthermore, for the detection heterogeneity parameter, we assumed a half-normal prior distribution centered on the mean detection probability (on the log-scale), with a variance of 1.66. This prior gave more weight to smaller values of the heterogeneity parameter but at the same time did not unduly constrain it. We conducted a prior sensitivity analysis and refitted the models under the assumptions that either there was no detection heterogeneity at all or that the half-normal variance was 10, i.e. that there was considerably more heterogeneity among territories being detected. All main conclusions (see below) were unaffected by our choice of priors. We used the Brooks–Gelman–Rubin Rhat statistic (an ANOVA-like measure which expresses the ratio of between chains variance to within chain variance) to check for convergence of our Markov chains, which we deemed acceptable if no parameter had a Rhat value greater than 1.1 (Gelman and Hill, 2007). We present posterior means and standard deviations (the Bayesian analogue of a frequentist MLE and SE).

The demographic trends of the two bird species in Finges were compared with their overall Swiss population trend index for the period 1990–2006 (A. hypoleucus) and 1994–2006 (C. dubius). Although the two data sets are based on different metrics (abundance vs. distribution), the strength of their inherent relationship validates our approach (Frisk et al., 2001). Trends were estimated using a linear regression analysis of the annual proportion of occupied 1 km² quadrats among those surveyed and recorded in the Swiss ID database (Kéry et al., 2010). Since the number of surveyed quadrats varied considerably among years, we weighed the regression with the inverse of the squared standard error of each annual proportion (Fox, 2002).

In order to look at correlations between the number of territories of the two bird species vs. habitat availability, we had to rely on pairs of approximately simultaneous years for bird surveys and habitat mapping. For the 1995 survey we went as far as to interpolate habitat availability from data obtained in 1992 and 1998. The resulting year pairs (bird vs. habitat) were: 1978 vs. 1981; 1987 vs. 1986; 1990 vs. 1992; 1995 vs. mean of 1992 + 1998; 1999 vs. 1998; 2007 vs. 2006. Due to the small sample size we used Spearman’s correlation tests in R 2.9.1 (R Development Core Team, 2009). Tests were one-tailed given the direction of prediction (increase of bird population sizes with expected increase of the area of riparian habitats). Results are presented as mean ± standard error of the mean.

3. Results

The overall area of riparian habitats (habitats 1–5) increased by 9% from 1981 to 2006 (Figs. 1 and 2). Major changes in the habitat mosaic were due to a progressive increase in the area of alluvial deposits with 10–50% of grass–bush cover (2.7-fold, habitat 3) and alluvial deposits with 50–70% of bush–small trees cover (+40%, habitat 4). Further positive changes concerned natural and artificial sand arms, which most of the time included temporary ponds (habitat 2, 4.1-fold increase from 88 ares (1981) to 198 and 363 ares in 1998 and 2006, respectively, with troughs of 20 and 19 ares in 1986 and 1992, respectively; Fig. 1]. During the revita- lization period, as much as a 19-fold increase was registered between 1992 and 2006, but starting from the very low level reached in the late 1980s and early 1990s. The proportion of lateral arms artificially created through targeted extraction of gravel and pebbles was 65% and 55%, in 1998 and 2006, respectively. The overall gain in surface area of pioneer riverine habitats was mostly at the expense of a decrease of the area of young riparian forests (Fig. 2).

The diversity of the habitat mosaic (habitats 1–5) decreased gradually during the pre-revitalization period (1 – $D = 0.46$ and 0.43 in 1981 and 1986, respectively), down to 0.36 in 1992, but...
increased again afterwards (0.38 and 0.57 in 1998 and 2006), reaching its peak over 26 years at the last habitat mapping in 2006.

The two bird species showed positive demographic trends between 1978 and 2007, with most positive changes occurring after 1990 (C. dubius) and 1999 (A. hypoleucos) (Fig. 3). According to our surveys, A. hypoleucos increased its number of territorial pairs from 11 to 21, and C. dubius from 2 to 12 since 1978. However, the probability of detection differed markedly between the two species and among the years (1995, 1999 and 2007) for which a capture–recapture model was fitted (Supplementary Figs. S1 and S2). For A. hypoleucos, 10, 12 and 21 territories were detected in 1995, 1999 and 2007, respectively, and for C. dubius, 8, 10 and 12 in the same years, respectively. For A. hypoleucos, correcting for imperfect detection yielded population size estimates for 1995, 1999 and 2007 of 11.1 (SE 1.9), 14.1 (SE 2.7) and 21.2 (SE 0.8), respectively, while for C. dubius increases were of 11.5 (SE 3.8) and 13.5 (SE 2.1) in 1995 and 2007, respectively (see Supplementary Figs. S1 and S2, left panels; the available information was not sufficient to provide adequate estimates for 1999 for C. dubius). Thus, we estimated that between 1995 and 2007, population increases were of 83% and 20% for A. hypoleucos and C. dubius, respectively.

Interestingly, detection probability was not constant over the years for either species (Supplementary Figs. S1 and S2, right panels). While there did not seem to be much difference between 1995 and 1999, there was a marked increase between these 2 years and 2007, with values at their highest in 2007. The difference in mean detection probability between these years was estimated at 0.26 (SE 0.13) for A. hypoleucos and at 0.29 (SE 0.21) for C. dubius. Based

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**Fig. 2.** Changes in the major habitat types (mapped from aerial photographs taken in 5 years as indicated) from 1981 to 2006 (Rhone river, Finges, Valais, Switzerland). Renaturation measures were implemented since 1994.

**Fig. 3.** Changes in the population sizes of two rare wading birds (A. hypoleucos and C. dubius) surveyed in Finges during 6 years between 1978 and 2007. The error around the population estimates represent the Bayesian error terms in species detectability obtained from a capture–recapture model constructed from the surveys carried out in 1995, 1999 and 2007. Only observed errors obtained from years with reliable surveys are depicted (see text for more details). The years with habitat mapping are indicated by the bars below the frame (Fig. 2). Habitat restoration began in 1994. Major floods events took place in 1987, and especially 1993 and 2000.
4. Discussion

This long term study of a segment of the river Rhone, spanning over three decades, quantitatively documents the positive effects of renaturisation on both the riverine habitat mosaic and emblematic, non-aquatic vertebrates typical of riverine ecosystems (Skinner et al., 2008). The majority of studies on river renaturisation demonstrated positive effects on biodiversity (but see Moerke and Lamberti, 2003), but restoration success tends to vary rather widely depending on revitalization method and catchment type (Palmer et al., 2010).

The study section of the river Rhone which had been progressively channelized, reaching a low in habitat diversity in the early 1990s, was converted back to a braided river from 1994 onwards, with a marked increase in habitat heterogeneity. It was essentially pioneer habitats characteristic of the early stages of vegetation succession which were promoted by the revitalization measures, while the area covered with woody plants decreased, as noticed elsewhere (Rohde et al., 2004; Ernst et al., 2010). This resulted in a positive demographic response of two rare indicator vertebrate species of river ecosystem integrity that depend on these pioneer habitats, as assessed by a capture–recapture Bayesian model that accounted for detection probability. Both the common sandpiper (A. hypoleucos) and the little ringed plover (C. dubius), which have, respectively, dramatically declining or more or less stable populations in Switzerland, showed marked increases in their population sizes after 1994. The fact that the revitalized section was rather long (8.8 km) (Pretty et al., 2003; Jähnig et al., 2010) and little disturbed by leisure activities was probably decisive for establishing sustainable populations of the birds. Contrary to the present study, Landmann (2007) could not demonstrate any positive effects of revitalization of a 14 km long stretch of the Lech river (Austria) on the same two wading bird species between 1989 and 2006, which may to some extent be attributable to a failure of accounting for probability of detection.

The capture–recapture model adopted for the survey data from the years when four visits were conducted (1995 and 2007) enabled to calibrate the probability of detection. This was rated as very good for the common sandpiper while less precise for the little ringed plover. This imprecision is reflected by much larger errors around the population size estimates in the latter species. The fact that detectability increased between 1995 and 2007 suggests that the number of antagonistic interactions between territories occurring at higher density rendered the birds more conspicuous to the observer. The magnitude of the change is so great that potentially counter-acting effects due to more distant sampling after river broadening were probably totally masked by positive density-dependent detectability. The species-specific differences in probability of detection (1995 and 2007) can be interpreted by a generally higher conspicuousness of common sandpipers compared to little ring plovers. The former have a larger body size and a slightly less cryptic plumage. They have a longer flushing distance, relying less on their camouflaged plumage; they also are generally more noisy, calling at higher intensity while flying, which enables to locate them despite the tumult of the stream. Finally, common sandpipers actively defend their whole home range contrary to little ring plovers that repel intruders mostly when these approach the nest (A.L., personal observations).

The importance of Finges is further emphasized by the fact that it provides extended natural habitats for C. dubius, for whom 40% of the breeding population in Switzerland is found in secondary (i.e., man-made) habitats such as gravel pits (Maumary et al., 2007).

4.3. Population changes

The population increases observed locally in Finges differed markedly from the general demographic tendencies obtained for Switzerland as a whole, where the two species showed either a distinct declining trend (A. hypoleucos; t1,18 = 24.30, p < 0.001) or no trend at all (C. dubius, t1,18 = 0.57, p = 0.57) during the last two decades (Fig. 4).

Notwithstanding the detectability effect above, and thereby assuming that our survey population sizes depict at least relative trends in population sizes, only one single significant species-habitat association was found (C. dubius). The number of its territories correlated positively with the availability of natural and artificial sand arms (r = 0.754, p = 0.042), which is the habitat showing a very large increase in area since the start of the renaturisation project. Assuming again that our surveys are representative, population densities were estimated based on the area of alluvial habitats (A. hypoleucos: habitats 1–4; C. dubius: 1–3). In A. hypoleucos, the average (±SD) yearly density was 1.13 ± 0.2 territories per 10 ha (range: 0.91–1.56, n = 6), with little variation over time and a maximum reached in 2007. In C. dubius, the yearly density varied more between years (0.59 ± 0.36; range: 0.21–0.98, n = 6), increasing progressively from 0.21 territories in 1978 to 0.98 and 0.97 per 10 ha, in 1999 and 2007, respectively.

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Fig. 4. Index of population changes for the two wading bird species surveyed in this study (A. hypoleucos and C. dubius) in Switzerland as a whole. The index is set to 100 for the reference year (2000).
A comparison of the recent population trends for the two wading bird species in Finges compared with their otherwise overall decline (A. hypoleucos) or stability (C. dubius) in Switzerland suggests that the increase in population size in both cases is likely due to changes in the availability of their preferred habitats. Assuming that our figures for population trends reflect the actual local demographics for the two species, the little ringed plovers would have to show an earlier response to habitat changes than the common sandpipers. In effect, the former species readily colonizes river ecosystems in their early stages of succession, showing a marked preference for bare alluvial habitats typical of post-flood conditions. This enables it to rapidly settle down in gravelly man-made habitats where water may even be absent (Maumary et al., 2007). C. dubius would thus have benefited from the major floods of 1987 (after which population starts to increase), 1993 and 2000, as well as from the revitalization measures which were implemented from 1994 onwards, because these factors would have massively promoted bare habitats (19-fold increase between 1992 and 2006). In contrast, the favourite habitats of A. hypoleucos only increased by minor factors (2.7-fold increase for alluvial deposits with 10–50% of grass and with some bush cover; 1.4 for alluvial deposits with 50–70% of bush and small trees cover). As A. hypoleucos is a later colonizer of vegetation succession in dynamic river systems, its population has increased more recently and may further increase in the future, as vegetation progressively colonizes the newly created bare habitats.

An important component of the river mosaic which may have played a major role in the positive development of these wading bird populations may be the presence of numerous sandy arms, most often harbouring temporary water bodies. Contrary to the river’s water which is cold and charged with sediments, these lateral arms have warmer, clearer water—outside the periods of high water discharge—mostly supplied by underground sources. Outside of the high water periods, the duration of these temporary water bodies thus largely depends on the proximity of the water table. In addition to sandy substrates and banks, these ponds trap numerous organic debris. The combination of fine-grained substrates, abundant organic material and shallow waters rapidly warmed up by solar radiation leads to a high productivity in communities of aquatic and semi-aquatic invertebrates, which represent the staple food of the two wading bird species. The progressive widening of the bed following the major floods that destroyed the main lateral levees, as well as the interventions with machinery operated within the river bed consisted in the main factors which created these numerous lateral arms, providing optimal conditions for the two bird species. The prime importance of lateral arms was already postulated by Pretty et al. (2003) and has recently been evidenced by studies on macro-invertebrates (Lorenz et al., 2009; Paillex et al., 2009).

Interestingly, the artificial excavation of these lateral arms, which aimed at avoiding excessive accumulation of sediments while mimicking natural river dynamics, provided room for a continuous exploitation of gravel and pebbles, a significant source of income for local stakeholders. This economic aspect certainly facilitated the acceptance of the management plan. Benefits for the wading birds were achieved by the controlled exploitation of gravel and pebbles in space and time by ecologists. Exploitation of alluvial deposits under the control of conservation biologists will continue, in response to the continuous accumulation of sediments along this stretch of the river (see Section 2), which warrants the availability of suitable habitats for the two waders in the long term. As these two wading birds are indicators of river ecosystem integrity, their proliferation might suggest a benefit for other wildlife. In effect, the management measures described have proven to boost other rare species of non-aquatic plants and invertebrates (Werner, 1998, 2005).

This study demonstrates how river bed widening may enhance ecological conditions for rare riverine wildlife typical of braided streams. It further shows that economic exploitation of river sediments, if managed properly, may contribute to support biodiversity. The persistence of biodiversity in sensitive dynamic ecosystems within intensively used landscape matrices may depend on the capacity of economy and ecology to work hand in hand to ensure both income for humans and better conditions for wildlife.

Acknowledgements

We thank Hans Schmid who calculated the Swiss bird population trend indices for the two bird species. GIS mapping of habitats has been carried out by Marie-Aude Faron and Bastien Amez-Droz. This study was financed by the Valais Office for National Road Networks in Sion. Thanks to Aliki Buhayer who revised the English and to anonymous reviewers whose suggestions greatly improved the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.biocon.2011.05.003.

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