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Authors: Hofer, Josef, Korner-Nievergelt, Fränzi, Korner-Nievergelt, Pius, Kestenholz, Matthias, and Jenni, Lukas

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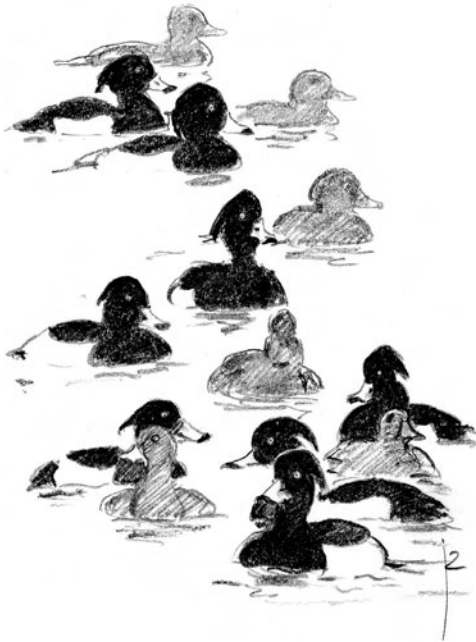
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An indication of long-term group formation in Tufted Duck *Aythya fuligula*

Josef Hofer¹, Fränzi Korner-Nievergelt^{2,3,*}, Pius Korner-Nievergelt^{2,3},
Matthias Kestenholz² & Lukas Jenni²

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Many waterbird species assemble in large aggregations during winter. In most species, these aggregations are generally thought to be composed of individuals not familiar to each other. In this study, we analysed mark–recapture data of Tufted Ducks *Aythya fuligula* and Common Pochard *A. ferina* from four wintering places in Switzerland to assess whether individual birds were recaptured non-independently of each other one or more years later. We found that individual Tufted Ducks caught together during a previous winter were re-caught together more often than expected by chance. Our results suggest that winter flocks of Tufted Ducks may be socially structured to an extent unknown so far. We discuss a number of hypotheses that could explain our observations, but clearly, much more work needs to be done to confirm our observation and to understand its causes.

Key words: *Aythya ferina*, *Aythya fuligula*, grouping behaviour, long-term pair bonds, waterbird, wintering

¹Seehäusern, CH-6208 Oberkirch, Switzerland; ²Swiss Ornithological Institute, CH-6204 Sempach, Switzerland; ³oikostat GmbH, Ausserdorf 43, CH-6218 Ettiswil, Switzerland;

*corresponding author (fraenzi.korner@vogelwarte.ch)

INTRODUCTION

Large aggregations of waterbirds often occur during winter around rich feeding places or safe resting sites (Bezzel 1959, Nilsson 1980, Scott & Rose 1996). Such aggregations may either consist of familiar or non-familiar individuals. Social structure can have several positive consequences for animal groups such as reduced aggressiveness within the group (Pusey & Packer 1997) or improved orientation or timing of migration due to common knowledge (Helm *et al.* 2006), explaining why familiar individuals might aggregate. Pair formation and grouping behaviour of families has been studied in ducks, primarily at the breeding site (Bezzel 1959, McKinnon *et al.* 2006). However, little is known about the social structure within waterbird aggregations outside the breeding season. For Tufted Ducks *Aythya fuligula* and Common Pochards *A. ferina*, for instance, there appear to be no studies that have investigated social structure in groups of wintering individuals.

Social structure within large wintering flocks is known to occur in swans (Cygninae) and geese (Anserinae), where families remain in contact outside the breeding period for several years (Elder & Elder 1949, Raveling 1969, Evans 1979, Ely 1993), suggesting that individuals can recognize each other. This has, for instance, been demonstrated in Greylag Geese *Anser anser* (Schwanke & Rutschke 1988). Most swans and geese and a few ducks such as Harlequin Ducks form life-long pair-bonds (Elder & Elder 1949, Raveling 1969, Evans 1979, Rohwer & Anderson 1988, Ely 1993, Regehr *et al.* 2001), and the same is true for duck species of the genera *Anas* and *Bucephala* (Savard 1985, Fedynich & Godfrey 1989, Mitchell 1997, Port 1998). In many species of these two genera, males abandon their mate following breeding but re-unite during winter (Rodway 2007a,b).

In *Aythya* ducks, there appears to be no recognition of related individuals beyond fledging (Bezzel 1959, Cramp 1977). For this genus, winter aggregations are thought to consist of individuals that are unfamiliar

with each other. In the Tufted Duck and Common Pochard, adult males leave their female and nest area prior to fledging (Bezzel 1959). In the wintering areas, up to several thousand kilometres from the breeding areas, these two species typically form aggregations of up to several thousand individuals (Bauer & Glutz von Blotzheim 1969, Bezzel & Hashmi 1989, Scott & Rose 1996). Here, we test whether such winter associations are random with respect to familiarity among wintering Ducks. We show here that individual Tufted Ducks caught together in one winter were recaptured together (same place, same day) in subsequent winters more often than expected by chance. We discuss a number of mechanisms that could lead to such social structure and outline evolutionary benefits of such structures for our studied species.

METHODS

Species, study sites and ringing procedure

The Tufted Duck is a primarily migratory species which breeds in the temperate zone of northern Eurasia (Cramp & Simmons 1977). In Switzerland, Tufted Ducks breed in small numbers but large numbers gather from October through April during migration and wintering. The highest numbers of Tufted Ducks are counted during December (Keller 2005). Numbers of Tufted Ducks have increased from around 40 000 in 1967 to around 200 000 in the 1980s and 1990s, and decreased to around 160 000 since 1997. During mid-winter substantial nocturnal flight activity of diving ducks has been observed (Kestenholz 1995), indicating that translocations between lakes are common in wintering Tufted Ducks.

Here we analyse data from four different ringing sites in Switzerland: Oberkirch at Lake Sempach (47°09'N, 8°07'E), Lake Lucerne (47°03'N, 8°18'E), Lake Neuchâtel (46°59'N, 6°55'E) and Vevey at Lake Geneva (46°28'N, 6°50'E). More than 27 300 Tufted Ducks were ringed at Lake Sempach between 1955 and 2007. Tufted Ducks were also ringed at Lake Geneva ($n = 882$) between 1973 and 2003, Lake Lucerne ($n = 152$; 1967–1976), and Lake Neuchâtel ($n = 188$; 1975–1988). At Lake Sempach and Lake Lucerne, ducks were caught in a baited fence trap (Hofer *et al.* 2005, U. Petermann, pers. comm.). At other study lakes, ducks were caught with a spoon net from a boat or a bridge at night (G. Gilliéron, J.-D. Blant, M. S. Jacquat, pers. comm.). At Lake Sempach, a single trap was open and checked nearly daily from 1 October through 30 April each year. Catching at the other three sites was

restricted from December through March (1–3 times per week at Vevey, 1–4 times per month at Lake Lucerne and Lake Neuchâtel). At all four sites, captured birds were marked individually with metal rings, provided by the Swiss Ornithological Institute, and released at site of capture. Upon ringing, age and sex were determined from plumage characters (Bauer & Glutz von Blotzheim 1969). In cases where sex could not unambiguously be inferred from plumage characteristics, identification of sex was based on examination of the cloaca.

Stopover durations were relatively short (range = 2 days to 2 weeks) during winter, possibly because of low food availability (*Dreissena*-mussel was not present in large numbers before 2003; Kestenholz 1995, JH, unpubl. data). Though data on stopover duration were not available for the other study lakes, durations at those sites were probably longer because *Dreissena*-mussel appeared between 1962 and 1974 in these areas (Suter & Schifferli 1988).

We applied the same analyses to data collected for the Common Pochard, which were caught and ringed at all four ringing sites using methods outlined above. Though we obtained fewer data from this species (numbers ringed at Lake Sempach $n = 15$ 150; Lake Geneva $n = 95$; Lake Neuchâtel $n = 5$; Lake Lucerne $n = 1$), these data were analysed because a comparison with the Tufted Duck data could help to interpret the observed patterns. The two species have a similar ecology (Bezzel 1959) and phenology in Switzerland, though the maximum Swiss winter population of Common Pochard is lower (80 000–120 000, Keller 2005).

Data selection and hypotheses testing

We selected recapture data of ducks ringed at one of the four ringing sites, ringed and recaptured between October and April, and recaptured at the site of ringing. We used these criteria to exclude summer recoveries (1% of all records), and to control for winter site fidelity as a possible mechanism for producing non-random association of individuals in our data (see below). We selected recaptures that took place at least one winter season after ringing, because we were interested in long-term associations of individuals rather than short-term ones. Finally, we only selected data for ducks that were ringed together (same site and date) with other ducks that met the criteria above. We refer to 'Date' as one specific day of a specific year (e.g. 23 February 2003), while 'Julian day' refers to a date independent of year (e.g. 23 February).

For the Tufted Duck, we had 833 ring recapture data of 377 individuals available to test our hypotheses (outlined below). Of these 833 recaptures, 602 were ringed

and found at Lake Sempach, 181 at Lake Geneva, 29 at Lake Lucerne and 21 at Lake Neuchâtel. Individuals ringed at the same site on the same date are defined to be members of the same 'ring group'. Our data contained 151 such 'ring groups'. For Common Pochards, we analysed data of 63 individuals in 30 ring groups.

If at least two individuals of a 'ring group' were recaptured together (i.e. same site and date) at least one winter season later, we refer to a 'group recapture'. If the same individuals were recaptured as a group in more than one subsequent winter, they were counted as a single group recapture. We call the number of observed group recaptures G_{obs} . We tested whether G_{obs} was higher than expected by chance using a randomisation test. To do so, we randomised the recapture Julian day of the individuals within each site separately. To account for the decreasing recapture probability with increasing interval of years between ringing and recapture due to mortality, year of recapture was not randomised. We counted the number of group recaptures (G^*) in $R = 4999$ randomised data sets, enabling us to obtain a reference set of possible numbers of group recaptures G^*_i ($i = 1, \dots, R$) given a random association of individuals. The median of G^* was our expected number of group recaptures under the assumption of random association of individuals at recapture (our null hypothesis). The 2.5% and 97.5% quantiles of the distribution of G^* gave a 95% acceptance region for the null hypothesis.

Using another set of randomisation tests, we assessed whether the number of group recaptures G_{obs} could result from individuals returning to the ringing site at about the same time each year (i.e. timing-of-migration effects). These tests were identical to the ones described above except that, instead of randomising the Julian day of recapture, we simulated a recapture Julian day by randomly selecting from within the interval $[d-k, d+k]$, where d equals the Julian day of ringing, and k was set to one of 7 values (ranging between 5 and 60) at different runs. If $d-k$ was before 1 October or $d+k$ after 30 April, we used 1 October or 30 April, respectively, as lower and upper limits for the interval. In this way, we simulated birds returning to the ringing site at a maximum of $\pm k$ days difference from the Julian day of ringing. For each value of k we performed $R = 4999$ randomisations and obtained the expected number of group recaptures G^* given random association of individuals and the 95% acceptance region as described above. Due to lack of knowledge, we sampled the temporal return difference (difference between Julian day of ringing and Julian day of recapture) from a uniform distribution $U(0, k)$. However,

the observed temporal return differences were not uniformly distributed (dark grey bars in Fig. 1). Therefore, in addition, we performed a third randomisation test. Here, the random Julian days of recaptures were obtained by randomly sampling temporal return differences from the distribution of observed temporal return differences. Next, the sampled temporal return differences were added to the Julian day of ringing, though we restricted the recapture dates to lie between 1 October and 30 April as outlined above.

We used the software package R 2.5.1 (R Development core team 2007). R-codes for the randomisation tests can be obtained from FK upon request.

RESULTS

For the Tufted Duck, G_{obs} was 24 group recaptures. Of those 24, 13 groups were recaptured one year after ringing, 8 after two years, 4 after three years and 1 five years after ringing. One group was recaptured in 3 different winters, explaining why these numbers add up to 26 instead of 24.

The observed number of group recaptures ($G_{\text{obs}} = 24$, corresponding to 15.9% of the 151 ring groups) is much larger than expected by chance (randomisation test, $R = 4999$, $P < 0.001$). By chance, a median number of 11 (7.3%) group recaptures (95% interval: 6–17) would be expected.

For the Common Pochard, only 2 of 30 ring groups were recaptured again together at least one winter season later. This number did not differ from the expected number of group recaptures under the assumption of independent association between individuals, which was 1 (95% interval: 0–3, randomisation test, $P = 0.25$).

Individual Tufted Ducks may be found together because they visit the same place each winter at about the same time. However, our second randomisation test revealed that the observed number of 24 group recaptures can be expected with reasonable probability ($P = 0.043$) only if individual birds return to the ringing site within the range of ± 17 days around the Julian day of ringing (Table 1, Fig. 1). Thus, if ducks come back with a difference of ± 17 days or less, the observed number of group recaptures can reasonably be attained by chance alone. Conversely, if absolute return differences were allowed to be larger than 17 days, significantly less than 24 group recaptures were obtained in our randomisation. Only a small proportion of ducks, however, returned to the ringing site within ± 17 days of the ringing day (dark grey bars in Fig. 1), implying that the observed number of group recaptures is not a conse-

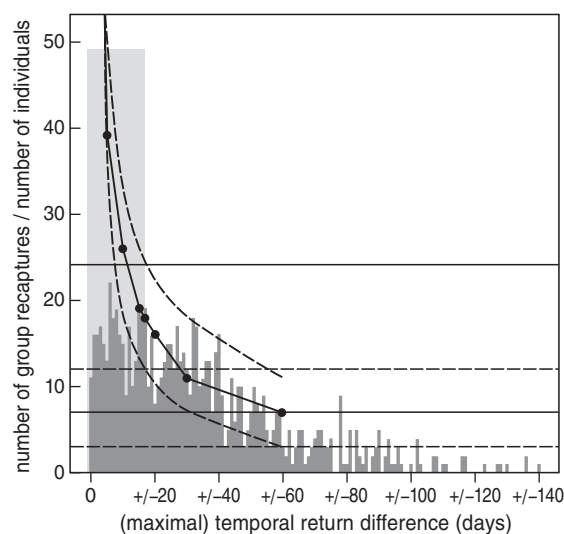


Figure 1. The number of expected group recaptures (black connected dots, read the y-scale as ‘number of group recaptures’) with 95% acceptance region (black broken lines) for different maximal temporal return differences taken from Table 1. Black horizontal line = observed number of group recaptures of Tufted Ducks ($G_{\text{obs}} = 24$). Dark grey bars show the distribution of the observed temporal differences (read the y-scale as ‘number of individuals’). For the maximal return error of 17 days (i.e. the threshold value above which our observed group recaptures cannot simply be explained by return precision, see text), the distribution of the individual temporal differences that underlie the simulation is given in light grey (uniform distribution $U(0, 17)$). Horizontal grey lines give the expected number of group recaptures (solid line) with the 95% acceptance region (broken lines) given the observed distribution of temporal return errors (i.e. dark grey bars). Reading example: If all individuals return to the site of ringing during a subsequent winter independently of each other and within a time interval of ± 17 days between ringing and recapture (distribution of differences between ringing and recapture = light grey), then we expect a median of 18 group recaptures (95% between 12 and 24) to occur just by chance.

quence of consistency in the time of return to the ringing site. The observed return differences ranged from 0 to 140 days (median = 28, $n = 833$). If we constructed the Julian day of recapture by adding a randomly chosen temporal difference from the observed differences between ringing and recapture Julian day (dark grey bars in Fig. 1), the expected number of group recaptures was significantly lower than the observed G_{obs} (median = 7, 95% interval: 3–12, horizontal dark grey lines in Fig. 1; randomisation test, $R = 4999$, $P < 0.001$).

The temporal return difference of the 63 individuals that formed the group recaptures ranged from 0 to 52 days (median = 19 days, $n = 63$). This median was significantly lower than the median difference of 28 days for all birds (Wilcoxon-test, $n = 833$, $P < 0.001$). Nevertheless, a median difference of 19 days between ringing and recapture was too large to explain 24 group recaptures by chance alone. A number of 24 group recaptures is achieved by chance only if every individual bird had returned within 17 days. However, comparison of the observed temporal return differences (median = 19, dark grey bars in Fig. 1) with a uniform distribution $U(0, 17)$ (light grey distribution in Fig. 1) shows that this was certainly not the case for our birds. The observed group recaptures were significantly more frequent later in the winter season than at the beginning (comparison of the observed number of group recaptures per month with the number of expected based on the total number of ringed Tufted Ducks in November through March: Chi-squared test: $\chi^2_4 = 17.3$, $P = 0.002$, Fig. 2). The sex composition of the observed group recaptures corresponded to a sex composition obtained if individuals were randomly chosen from a population with a sex ratio of 2.3 : 1 males, as it was observed in our data set.

Table 1. Results of randomisation tests used to assess the relationship between a given temporal return difference (first column) and the corresponding number of group recaptures expected if individuals had associated randomly (second and third column). The P -values give the probability of the observation of 24 group recaptures of Tufted Ducks under the assumption of random association between individuals and the maximal temporal return difference. The expected number of group recaptures and the acceptance regions are graphically displayed in Fig. 1 (black connected dots and black broken lines).

Maximal temporal return difference k (days)	Expected number of group recaptures, median of G^*	95% acceptance region	P -value
± 5	39	[32, 48]	1
± 10	26	[18, 33]	0.73
± 15	19	[13, 26]	0.11
± 17	18	[12, 24]	0.043
± 20	16	[10, 22]	0.009
± 30	11	[7, 18]	< 0.001
± 60	7	[3, 11]	< 0.001

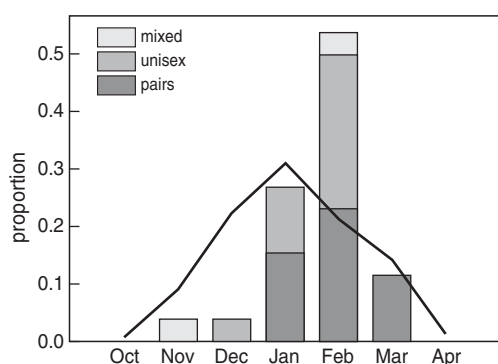


Figure 2. Seasonal distribution of the group recaptures (bars, $n = 24$) and of the total number of Tufted Ducks ringed (line, $n = 14\,706$). The shading of the bars indicates the proportion of the number of recaptured groups consisting of one sex only ('unisex'), of pairs (i.e. one male and one female), and other combinations (i.e. at least three individuals and not all of the same sex, 'mixed').

DISCUSSION

Our analyses revealed non-random, inter-annual associations of individuals in wintering flocks of Tufted Ducks. Groups captured together in one winter were more likely to be recaptured together in subsequent winters than would be expected by chance. In contrast to the Tufted Duck, no such pattern was observed in Common Pochards. To our knowledge, our results constitute the first indication of multi-year associations of individuals in an *Aythya* species.

Individuals that were ringed as a group might be recaptured at the same location and day because of consistency in timing of migration of individual birds. In this way, individuals would visit the same place at about the same time each year, thereby increasing the chance to be recaptured together even in the absence of any specific group formation. Winter site fidelity (e.g. Leuzinger 1996, Baccetti *et al.* 1999, Iverson *et al.* 2004) and stopover site fidelity (e.g. Bishop & Warnock 1998, Kruckenberg & Borbach-Jaene 2004) have been described for many wader and waterfowl species. Consistency in timing of migration of individual Bewick's Swans *Cygnus columbianus* has also been observed (Rees 1989). In Blackcaps *Sylvia atricapilla*, different timing of migration even causes non-random mating (Bearhop *et al.* 2005). However, our randomisation tests showed that consistency in timing of the return to the ringing site alone cannot account for the number of observed group recaptures (Table 1, Fig. 1). Nevertheless, individuals recaptured in a group

returned on average 9 days closer to the day of a previous capture compared to all individuals. This pattern might suggest that individuals migrating in groups have a higher consistency in their timing of migration due to common knowledge (see Helm *et al.* 2006).

Individuals might adjust timing of migration according to weather patterns on a continental wide scale, so that they return more or less together but around different Julian days each year depending on weather. This hypothesis requires that philopatric individuals show a similar reaction to large-scale weather phenomena across a large geographic area. Individuals may start from common breeding areas, moulting places, or wintering areas, and therefore pass by our study sites more or less synchronised. Such synchrony would be expected to dissolve with time after takeoff. We registered most group recaptures towards the end of the winter (Fig. 2). Therefore, winter site fidelity combined with synchronous start of spring migration might be an explanation for our observation. However, Tufted Ducks are known to be very mobile during winter (Kestenholz 1995, Korner-Nievergelt *et al.* 2009), regularly moving >200 km within a few days. This behaviour would diminish the synchrony of individuals and, concomitantly, the chance to accidentally obtain group recaptures. Therefore, our observations indicate that Tufted Ducks might rather re-group during the winter season than arriving synchronously at the ringing sites due to a common departure area.

Tufted Ducks might recognise each other individually and, at least part of the birds, might re-group with familiar individuals in winter. Consistent with this idea, individual recognition has been recorded in Greylag Geese (Schwanke & Rutschke 1988) and other bird species (Falls 1982, Reed 1985, Laiolo *et al.* 2000). Groups of familiar individuals might be restricted to kin members, or, alternatively, ducks might recognize individuals with which they aggregated in a previous winter. Our groups were neither typically same-age birds nor pairs (Fig. 2; note that we use the term pair for 'exactly one male and one female of the same ring group recaptured together'; we do not use behavioural traits to determine a pair), which makes it rather unlikely that our groups represented exclusively siblings or breeding pairs, respectively. Nevertheless, groups might be family members, as documented for the Greater White-fronted Goose *Anser albifrons* (Miller & Dzubin 1965, Ely 1993). Furthermore, in the Common Eider *Somateria mollissima* social groups were composed of genetically-related females (McKinnon *et al.* 2006). An avenue for future study is the research on relatedness among Tufted Duck captured in groups.

A lack of group recaptures during autumn migration suggests that Tufted Duck groups separate during summer and regroup during winter. This suggestion is illustrated by a single anecdotal observation of a group recovery during spring migration, when two males ringed on 11 March 1987 at Lake Sempach were shot one year and two months later within three days (15 and 18 May 1988) at the same place in Russia, 3111 km from the ringing site. Groups might be formed during courtship time, i.e. from January onwards (80% of the females are paired in March, Bezzel 1959, Rodway 2007a). Thereby, long-term breeding pairs might reunite and might be joined for a yet unknown reason by familiar individuals. This could explain why our groups were not predominantly pairs but instead consisted of 2 to 5 individuals with no obvious pattern in relation of age and sex composition. Seasonal occurrence of group recaptures coincided closely with courtship time in Tufted Duck (January–spring), providing an explanation for why we did not find non-random associations in Common Pochards. Courtship time in Common Pochards starts later in the season (February) with most females remaining unpaired until May (Bezzel 1959, Rodway 2007a), implying that many leave our study area unpaired.

The explanation of re-uniting long-term pairs causing non-random associations is supported by the notion that long-lived species are more prone to have long-term pair bonds (Rodway 2007a). In contrast to Common Pochard, Tufted Duck is among the *Aythya*-species with the highest annual female survival (0.71, Rodway, 2007a). It is known for most Mergini, and suggested for some Aythini (Rodway 2007a), that pairs reunite in winter.

In conclusion, we observed more group recaptures in wintering Tufted Ducks than expected by chance. At present, we do not yet understand the causes of these non-random associations. However, our findings suggest that socially-structured groups might exist within the large assemblages of wintering Tufted Ducks, and that this is where non-breeding individuals can relocate familiar individuals from previous winters.

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SAMENVATTING

Watervogels komen in de winter in grote groepen voor. Bij de meeste soorten bestaan deze groepen voornamelijk uit individuen die elkaar niet kennen. In het onderhavige onderzoek werden vangst–terugvangstgegevens van Kuifeenden *Aythya fuligula* en Tafeleenden *A. ferina* uit vier overwinteringsgebieden in Zwitserland gebruikt om te bepalen of in latere winters individuele vogels onafhankelijk van elkaar werden teruggevangen. Kuifeenden die in een voorafgaande winter samen waren gevangen, bleken vaker samen teruggevangen te worden dan op basis van toeval werd verwacht. Deze resultaten zijn een aanwijzing dat groepen Kuifeenden in de winter een sociale structuur kennen die tot dusver nog niet was opgemerkt. (NJD)

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