Habitat use and home range size of autumn staging radio-marked Teal Anas crecca at Ulvshale-Nyord, Denmark

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Abstract

Optimal design and management of wetland reserves requires knowledge about how individual waterbirds exploit such sites and how different factors influence patterns of habitat use. To understand more about how Teal *Anas crecca* use shallow Danish coastal wetlands during autumn migration, 252 individuals were radio-tagged and tracked daily at a major staging site during September–December in autumns 1995–2001 inclusive. Teal generally preferred the same habitats by day and at night, but the relative use of shallow waters and saltmarsh varied extensively between years, mainly due to year-to-year variation in water levels in the shallows. Home ranges and movements were analysed for 142 individuals located on at least 10 occasions. There was no evidence for sex- or age-related differences in home range size and movements despite considerable individual variation. Based on 3,239 individual radio positions, largest home ranges corresponded with seasons when low water levels allowed most access to shallow coastal waters and to more extensive feeding opportunities generally. High water levels constrained Teal to rest and feed in saltmarsh areas throughout the day and night.

Key words: home range, movements, radio-tracking, reserve, saltmarsh.

Effective design and management of wetland reserves requires an understanding of how individuals exploit the sites and the factors which influence their patterns of habitat exploitation. Teal *Anas crecca* is an important quarry species throughout Europe, and its abundance at key autumn staging areas is often amongst the criteria for

the designation of protected sites under national and international nature conservation legislation. Despite this, remarkably little is known about how these birds exploit various habitats during migration, either in spring before reaching breeding areas (Arzel *et al.* 2006) or during autumn staging, when post-breeding Teal accumulate stores for migration to their winter quarters. Such knowledge is important in attempts to optimise the habitat quality, availability and extent for these waterbirds. In order to understand how individual birds utilise the range of habitats available to them during an autumn stopover period, there is also a need to understand the functional use of habitat elements exploited by Teal (sensu Tamisier 1978; Tamisier & Tamisier 1981); for instance, the benefits to the Teal of exploiting particular comfort/ resting areas in relation to those areas used for foraging. Whilst some of these processes are well known from radio telemetry studies on the wintering grounds (Guillemain et al. 2002; Legagneux et al. 2009), there is little such information to better manage autumn staging sites.

This study investigated site use by Teal at a major autumn staging area in southeast Denmark by fitting individuals with VHF radios, then tracking their subsequent movements. The objectives were to determine how autumn staging Teal exploit shallow coastal wetlands, specifically to: 1) measure individual variation in home range size and habitat use, 2) assess whether there were differences between age and sex classes in home range size and habitat use, 3) determine whether home range size and habitat use was related to timing of staging, and 4) to compare differences in habitat use between years and between night and day.

Methods

Study area

Ulvshale-Nyord (55°02'N, 12°4'E) is part of the large c. 100 km² site designated as a

Special Protection Area for birds under the EEC Birds Directive and as a Ramsar site "Præstø Fjord, Jungshoved Nor, Ulvshale and Nyord" in southeast Denmark (Anon 1995). The study area consists of shallow brackish water around coastal areas (hereafter referred to as "shallows", mainly < 80 cm deep), with adjacent small islets, saltmarsh and additional areas of wet grassland, reed swamp (Phragmites australis with peripheral Sea Club-rush Scirpus maritimus), woodland and farmland (Fig. 1). In the saltmarsh areas, Saltmarsh Rush Juncus gerardi, Creeping Bent Agrostis stolonifera and Red Fescue Festuca rubra dominate the upper parts, whereas the lower marsh is colonised by the annuals Glasswort Salicornia sp. and Sea-Blite Suaéda maritima during summer. The saltmarsh, which is grazed by cattle to the end of October, includes large creeks with several small and a few large (up to 11 ha) saltpans. Inundation and filling of the saltpans with water (which makes them highly attractive to feeding and loafing Teal) varies markedly between years, partly due to variation in early autumn precipitation, but more especially due to the timing and extent of flooding caused by high water levels. There are extensive shallow waters along the coast, with silt sediments partly covered by a well-developed community of submerged macrophytes, predominantly Tasselweed Ruppia sp. and Fennel-leaved Pondweed Potamogeton pectinatus in the shallow areas (at depths from 5-10 cm to c. 100 cm), and with Eel-grass Zostera marina in deeper waters (depth > c. 100 cm, Madsen et al. 1992). In this part of the western Baltic, the lunar tide only causes a difference of c. 15 cm between low and high tides. However, during the



Figure 1. Geographical distribution of Teal at Ulvshale-Nyord based on radio-tracking positions gathered during autumn 1998 (upper) with generally high water levels and 1999 (lower) with generally low water levels, shown in relation to extent of the main habitats available in the area and the catching site for all birds (*i.e.* Tyreholm).

study periods water levels could change gradually over several days or shift by 1–93 cm within a single or a few days, after which water levels could remain high or low for several weeks. Such changes in water levels were mainly caused by wind conditions in the North Sea, Skagerrak and further east in the Baltic. Consequently, extensive areas of mudflats and shallow waters were available to the birds in years with prevailing easterly winds, but not in other years dominated by westerly winds, and this has marked effects on the accessibility of submerged plants to foraging waterbirds (Clausen 1998, 2000).

Hunting was prohibited in parts of the saltmarsh and over an extensive area of the shallows south of Nyord and Ulvshale (Madsen 1998). Human activity on the saltmarsh was limited to tending cattle and fences, though hunting took place in the evening once every 1–3 weeks during 1998–2001 (see Bregnballe & Madsen 2004). Apart from hunting from punts on the water north of Nyord and Ulvshale, human activity on the shallows was limited to tending fishing nets (pound nets) 1–2 times/day.

Teal use Ulvshale-Nyord as an autumn staging area, and there is substantial variation between individuals in the amount of time that they spend at the site (unpubl. data from radio tracking and see below). First arrivals occur in August, with peak arrivals in September and the first half of October. There is another modest arrival of further birds in late October/early November and the species departs with the first heavy frosts, usually in early December (Madsen *et al.* 1992; Bregnballe *et al.* 2005). Annual maximum numbers counted during the autumn migration period varied from 1,500–3,700 during the study years (1995–2001).

Radio marking and tracking

Teal were caught in baited swim-in funnel traps situated in shallow pools on the reedfringed island of Tyreholm, southeast of Nyord (Fig. 1) on four successive days at 2-3 week intervals each autumn, mainly from mid-September until November in 1995-2001. About two-thirds of the birds were caught in September-October. A total of 252 individuals were marked with Biotrack SS-2 or TW-4 or Holohil PD-2 transmitters (weighing 3.5-3.8 g, corresponding to c. 1-1.5% of Teal body weights) by gluing onto the back and back feathers. A handheld 3-element Yagi directional antenna and either Mariner M-57 Biotag or Teleonics TR-4 tracking VHF receivers were used to search for tagged birds. An observer regularly visited each of seven standard observation points around the study area to search systematically for radio signals. The positions of tagged birds were determined by triangulation based on the angle of the strongest signal strength from 2-3 of the nearest observation points for each transmitter. Exceptionally, when tagged Teals were located away from their normal haunts, searches were made from 1-3 additional points to obtain accurate triangulations. Two or three searches were undertaken almost daily during September-December. The first (morning) session was started 1.5-2 h after sunrise; the second (afternoon) timed to finish at least 1.5 h before sunset and a third 1.5-2 h after sunset. The Biotrack TW-4 transmitters had

a range of 3-4 km but in 2000 and 2001 Holohil PD-2 transmitters with a range of 5 km were used. Despite these differences in radio transmitters and receivers, 99% of all determined positions fell within 3 km of the observer and there were no differences in overall detectability functions of the different equipment combinations. An area of 6×10 km was covered, including the vast majority of suitable habitat available within a radius of 10 km of the capture site. A few Teal may have moved to small wetlands > 10 km from the central study area (especially at night), beyond the range of the transmitters. The individuals caught and released with transmitters were assumed to be a mix of birds that had recently arrived and birds that had been present in the area for a few or several days.

Data analyses

Each of the positions identified from triangulation were allocated to a cell of 1 ha in a grid covering the entire study area. The main habitat present in each cell was identified from aerial photos and for some cells from on-site visits. Positions recorded between sunset and sunrise were categorised as positions from night-time and all other positions as positions from day-time. Home range size, movements and habitat choice were calculated from 3,239 positions for 142 individuals (92 adult females, 26 juvenile females, 15 adult males and 9 juvenile males) that were located on 10-66 occasions (median = 17) on 5–96 days (median = 16)days) in the same autumn. The time interval between successive positional fixes obtained from each of the transmitters varied, although 72.6% of these were within the range 2-24 h. The frequency distribution of the time intervals beyond 24 h were: 24-48 h = 16.6%; 2–4 days = 7.3%; > 4 days = 3.5%. There is no doubt that some of the individuals that escaped detection during one or more successive searches were present but undetected because it was sometimes impossible to receive the signal from the transmitter at the standard observation points, possibly because of physical barriers in the landscape or because the angle of the antenna on the transmitter affected the transmission of the signal. Evidence for this presumption came from field trials where attempts were made to receive signals from transmitters artificially placed at a number of locations known to be used by Teal. The angle of the transmitter and its antenna was also experimentally manipulated at these locations and affected detecting probability. Because of these methodological difficulties it is not possible to state whether or not individuals that were undetected for a few or several days had temporarily moved outside of the study area or had been present in the study area at locations from which it was difficult to receive the signals.

Individual home range sizes were estimated as Minimum Convex Polygons (MCP), *i.e.*, the smallest polygon which can be drawn around the locations, giving an indication of the maximum extent of the total area in which birds were observed (Legagneux *et al.* 2009). Mean distances between positions were calculated for the entire duration of stay for each tracked individual.

Generalised Linear Modelling was used to determine environmental factors affecting habitat use by tagged individuals. Because it was suspected that Teal may exploit different habitats by day and night and that water level greatly affected availability of habitat, a model was made of the arcsine square root transformed probability of all positions in different years occurring on the two dominant habitat based on mean water level (measured at the time of each position), factoring in year and whether observations were by day or night. RSOUARE/AIC functions in PROC REG of SAS 9.1.3 were used to select between candidate models, using differences in Akaike's information criterion to aid model selection. A similar approach was used to model factors affecting the observed size of the home range used by the individual radiomarked Teal. The log-transformed home range area (logMCP measured in km²) was modelled using the following variables: year, age and sex of the individual as separate categorical variables, mean seasonal water table level, variance of seasonal water table level, difference between seasonal maximum and minimum water table level, mean daily distance travelled, length of stay, ringing date and median date between ringing and "departure" when signals ceased. Autumnto-autumn variation in home range size was analysed with an ANOVA using logtransformed home range area to normalise data.

Results

Habitat use

Saltmarsh (including saltpans and creeks) and shallow waters (including mudflats) were the preferred habitats, accounting for

90% of all positions recorded for the Teal. Other habitats exploited were reed beds (9.6%), grazed meadows (0.2%) and freshwater lakes (0.2%). Teal generally remained in shallow water areas when water levels were low, resorting to saltmarsh mainly when water levels rose, although the saltmarsh was used more frequently after flooding or heavy precipitation early in autumn. The distribution of positions of tagged Teal in 1998 (low water; extensive roosting and feeding in shallow waters) and 1999 (high water: birds confined more to the saltmarsh and shorelines) relative to the different habitat types are shown in Fig. 1 as examples of years with contrasting water levels. In 1999-2001, shallow waters and mudflats were used predominantly (Fig. 2). Year-to-year differences were due mainly to changes in overall water levels. Based on data from 1995-2001, AIC model selection favoured models predicting the percentage use of low water areas and saltmarsh which included year and mean water table as explanatory parameters, whilst day/night did not contribute significantly to models (Table 1). The parsimonious adoption of the simplest models (i.e. using only water level) resulted in models explaining 42% $(F_{1,13} = 8.7, P = 0.012, \text{low water})$ and 51% $(F_{1.13} = 12.7, P = 0.004, \text{ saltmarsh})$ of the variance in use of these two habitats. A plot of the proportion of each autumn position recorded on the shallows as a function of mean water levels suggests that there was a threshold water level above which Teal "suddenly" shifted from foraging and roosting on shallows to occurring on saltmarsh. Thus the proportion of positions on the shallows was 61-88% (data from day



Figure 2. Percentage of positions from radio-tagged Teal on: (A) shallow water (including mudflats and sandbars) and, (B) saltmarsh (including saltpans), as a percentage of all those from all habitats used during each autumn, September–December. Data are separated into daylight (white) and night-time (grey) hours. The lower figure (C) gives the mean water level (cm DNN, Danish Ordnance Datum) measured at the time of each position.

and night pooled) in the four autumns with mean water levels below 11 cm but 8-25% in the three years with water levels above 15 cm. Similarly, the proportion present on the saltmarsh increased from 2-24% to 63-73% with the shift in mean water levels from < 11 cm to > 15 cm.

Generally, Teal did not shift from their

daytime distribution at night (Fig. 2); on accounting for the effects of water level on Teal distribution, the explanatory categorical variable day/night did not contribute to explaining the variance in distribution between the two dominant habitat types (above). However, the results indicated that in years with low water levels numbers of **Table 1.** Model selection showing R^2 and AIC values for each of the candidate GLM models and their parameters fitted to explain the variation in the proportions of radio-marked Teal using the two most exploited habitat types (saltmarsh and low water habitats) at Ulvshale-Nyord, southeast Denmark.

Variables included in model (n)	Saltmarsh		Low water	
	R ² values	AIC	R^2 values	AIC
Mean water level (1)	0.514	-38.23	0.412	-29.07
Year (1)	0.562	-39.76	0.596	-34.13
Day/night (1)	0.001	-28.20	0.010	-21.59
Year Mean water level (2)	0.724	-44.20	0.692	-35.99
Day/night Mean water level (2)	0.514	-36.31	0.429	-27.31
Day/night Year (2)	0.563	-37.79	0.606	-32.48
Year Mean water level Day/night (3)	0.725	-42.25	0.702	-34.41

ducks on the saltmarsh tended to increase at night (Fig. 2), suggesting that some birds rested (and maybe foraged) by day on shallow water but still resorted to land to forage at night. There was no indication of such a day to night-time shift in habitat choice in autumns with high water levels (Fig. 2).

In autumn 1995, and 1998, high water levels and inundated saltpans provided good feeding conditions in saltmarshes and radiotagged Teal were almost entirely registered there. In contrast, in autumn 1999 and 2000, water levels were far lower than normal, the saltmarshes were dry and the salt pans empty throughout most of the autumn. In these years the Teal occurred mainly on the shallow offshore areas south of Nyord and around the island of Tyreholm.

Movements and home range size

The distance between successive positions ranged from an individual average of 235-2,878 m ($\bar{x} = 876$ m, 95% C.I. ± 37.7 m). Movements were greatest in 1999 and 2000 (mean distances between positions = 1,030m 95% C.I. \pm 105.7 m and 1,155 m \pm 84.1 m, respectively), when home ranges were also larger. Typically, individuals moved most around the area in the first few days after release, usually settling to remain in a smaller area (Fig. 3). However, the individual variation in movement patterns was extensive with some individuals moving little and using small home ranges initially but moving more extensively later (see examples in Fig. 4). Differences in the distance individuals moved could not be analysed by



Figure 3. Mean distance between successive positions (m \pm 95% C.I.) for all radio-tagged Teal staging at Ulvshale-Nyord during 1995–2001 as a function of position number during September–December (one-way ANOVA, $F_{7,2162} = 8.06$, P < 0.0001; same letter indicates no significant difference between means, based on Duncan multiple range tests at values for P < 0.05). Time between successive positions ranged from 2–48 h.



Figure 4. Cumulative distance moved (km) for one radio-tagged adult female (◊) and one young female (•) staging at Ulvshale-Nyord for approximately three weeks in autumn 1997.

age and/or sex because of the uneven representation of age and sex classes between different years, but there was no obvious sign of age or sex differences.

Home range size varied between 0.2-29 km^2 ($\bar{x} = 3.4 \text{ km}^2$ 95% C.I. $\pm 0.57 \text{ km}^2$). An analysis of the relationships between home range size and age, sex, year, ringing date, median date of individual fixes, mean water level during the autumn, variation in water level (variance and difference between maximum and minimum) and length of stay of the individual showed that water level parameters, distance travelled by the individual between fixes and length of stay were the dominant factors explaining the variation (Table 2). As the 18 first models provided similar fit, *(i.e.* differed by < 2 AIC units), it seems reasonable to focus on the most parsimonious model (n = 3 in Table 2). The most parsimonious model incorporating variance in water level, distance travelled and length of stay explained 60% of the variance $(F_{3,144} = 70.4, P < 0.0001)$ compared to a selected model using AIC criteria which incorporated more water level parameters but only explained a further 1.5% of the variance in home range size. Overall, it would therefore appear that home range size is less related to the age, sex and timing of staging for each individual but has more to do with the variation in the water table and its effect on local movements.

There were significant differences in average home ranges between years (oneway ANOVA, $F_{6,135} = 7.15$, P < 0.0001), 2000 being significantly greater than all other years except for 1999, which in turn was significantly higher than 1995 and 1998 (Tukey's Test, t = 4.23, P < 0.05). Year-to-year variation in distance between positions and home range size in autumn were inversely correlated with mean autumn water level (Fig. 5); high water levels restricted the availability of habitat and thus probably movements. Amalgamating all age and sex classes in all years, there was a significant positive correlation between duration of stay and home range (both measured by radio-tracking; Spearman rank, r = 0.26, P < 0.002, n = 142).

Discussion

Although the movement, home-range and length of stay of radio-tagged Teal at Ulvshale-Nyord showed considerable individual variation, there were no clear effects of age or sex on these patterns. The lack of age effects was unexpected, since it might be predicted that the more exploratory and less risk-averse behaviour of juveniles may result in greater movements, larger home ranges and perhaps shorter length of stay than amongst adults. However, since Teal are highly gregarious, it may be that associations between birds within flocks minimise agespecific responses.

The results suggest that individual Teal have different strategies for exploiting autumn staging sites, but that water levels (and thus food availability) were the dominant factor affecting habitat choice and the degree of movement during their stay at this autumn staging site. Teal tended to prefer to feed and roost in the shallow waters around the coast of Ulvshale-Nyord but these areas are only accessible to them when low water levels permit. In years with **Table 2.** Model selection showing R^2 and AIC values for each of the top 20 best candidate GLM models (ranked by AIC) and their parameters fitted to explain the variation in the logarithmically transformed home range areas used by each individually radio-marked Teal at Ulvshale-Nyord, southeast Denmark. Parameter codes are mean seasonal water table level (MeanW), variance of water table level (VarW), difference between seasonal maximum and minimum water table level (AmplW), mean daily distance travelled (Dist), length of stay (LOS), ringing date (RingDate), median date between ringing and departure (MedDate). Given that MeanW, VarW and AmpW are highly correlated, that VarW, Dist and LOS figure in all but one of selected models and that they explain a very high proportion of the variance compared to more parameterised models, we can be confident that these three variables explain much of the variance in the home range size of individual tagged Teal.

Variables included in model	<i>R</i> ² values	AIC	No. of model parameters
MeanW, VarW, AmplW, Dist, LOS	0.615	-422.53	5
Age, MeanW, VarW, AmplW, Dist, LOS	0.619	-422.06	6
Year, MeanW, VarW, AmplW, Dist, LOS	0.619	-422.01	6
Age, VarW, AmplW, Dist, LOS	0.614	-421.98	5
MeanW, VarW, Dist, LOS	0.608	-421.87	4
Age, Year, MeanW, VarW, AmplW, Dist, LOS	0.624	-421.72	7
Sex, MeanW, VarW, AmplW, Dist LOS	0.618	-421.45	6
Age, VarW, Dist, LOS	0.607	-421.40	4
Age, MeanW, VarW, Dist, LOS	0.612	-421.37	5
VarW, AmplW, Dist, LOS	0.607	-421.28	4
Age, Sex, MeanW, VarW, AmplW, Dist, LOS	0.622	-421.09	7
Age, Year, VarW, AmplW, Dist, LOS	0.617	-421.06	6
Age, Sex VarW, AmplW, Dist, LOS	0.617	-421.01	6
VarW, Dist, LOS	0.600	-420.78	3
Sex, Year, MeanW, VarW, AmplW, Dist, LOS	0.621	-420.58	7
MeanW, VarW, AmplW, Dist, RingDate, MedDate	0.615	-420.55	6
MeanW, VarW, AmplW, Dist, MedDate, LOS	0.615	-420.55	6
MeanW, VarW, AmplW, Dist, RingDate, LOS	0.615	-420.55	6
Year, MeanW, VarW, Dist, LOS	0.610	-420.47	5
Age, Sex, Year, MeanW, VarW, AmplW, Dist, LOS	0.625	-420.35	8



Figure 5. Annual mean home range size (km² \pm 95% C.I. identified to year) for the 142 radio-tagged Teal staging at Ulvshale-Nyord during September–December 1995–2001 in relation to mean daily water levels during September–December (r = 0.81, P < 0.05 based on annual mean data only).

sustained high water levels, these areas are too deep to permit Teal access to feeding resources in the shallows, but conversely the higher level saltmarshes and saltpans of the site become partially inundated (a phenomenon also associated with heavy precipitation even during low water conditions) and Teal resort to these areas as roosting and feeding habitat. There are apparently periods when inundated saltpans are preferred by some Teal even over partly exposed mudflats, suggesting that if these habitats are in suitable hydrological conditions, these may be favoured over all other habitats as feeding and loafing areas both by day and night. However, the birds are likely to be exposed to greater risk of predation on the saltmarshes, because the saltpans and saltmarsh are regularly hunted by White-tailed Eagles Haliaeetus albicilla, Harriers *Circus cyaneus* and *C. aeruginosus* and Peregrine Falcons *Falco peregrinus*. Here, patchy vegetation cover enables predators to take the Teal by surprise, which is not the case when the birds are on open water. Hence, although the saltmarsh may offer good feeding opportunities during periods of the autumn (Therkildsen & Bregnballe 2006), its attractiveness might partly be offset by the associated elevated predation risk. This might explain the observed higher percentage of diurnal time allocated to foraging activity in shallows in the study area (42%, Madsen *et al.* 1992) compared to saltmarsh (20–39%, Bregnballe *et al.* 2005).

On average, individuals moved longer distances between successive positions during the first few days after capture and release (Fig. 3). There may be at least two explanations for this. Firstly, it is likely that some radio-tagged Teal were caught soon after their arrival and that these individuals, new to the site, initially explored foraging and roosting opportunities within the area. Secondly, it cannot be excluded that capture and being marked with transmitters affected the birds' movements in the first few days following release.

Our studies showed that Teal broadly remained in the same general area and habitat type during the day and night. Guillemain et al. (2002) also found that wintering ducks remained in the same place throughout the 24 hours when undisturbed and when feeding conditions permitted. Other studies have shown that Teal move daily from daytime roosting reserves to distant feeding sites, which they only exploit during the night to reduce the risk of being shot by hunters (Fog 1968; Tamisier & Tamisier 1981; Euliss & Harris 1987; Legagneux et al. 2009). In the extreme, Teal autumn and winter feeding areas may be more than 20 km away from safe daytime roosts (Fog 1968; Tamisier 1985). Many reserves in the non-breeding range of Teal are daytime resting places which are not suitable for feeding, forcing birds to seek foraging sites outside hunting-free areas where they are subject to hunting disturbance and mortality. Hence, the configuration of adequate protected feeding and roosting areas would appear to save the Teal considerable energy through reduced commuting between otherwise spatially separated feeding and safe roosting areas. Although no searches for the marked birds were conducted during night at these distances from the day-time localities, the general presence of the birds in the same

areas by day and night suggests they were not regularly making such sorties. Some birds did, however, disappear for several days and nights before turning up again, which may suggest longer movements between periods spent at the site. Generally, however, birds remained in the local vicinity for prolonged periods in all years before a final departure.

At Ulvshale-Nyord, the designation of hunting-free areas that embrace areas of saltmarsh and the shallow coastal areas enable Teal to remain and feed, rest and indulge in comfort activities (Houhamdi & Samraoui 2001) in these habitats throughout the day and night without being subject to disturbance. This presumably minimises energetic expenditure during a period of fat store accumulation for onwards migration to the winter quarters, which generally are in western France (Clausen et al. 2002; Bønløkke et al. 2006). Assuming equal availability and quality of feeding resources, this ability to remain on feeding areas throughout the day and night may affect the degree of onward movement and the length of stay at this autumn staging area compared to others without such opportunities for the birds, where the Teal must commute between safe daytime loafing areas and night-time feeding areas. However, it is not clear as to what role predation and density dependence may affect habitat use and/or length of stay in situations where Teal remain longer and longer at such an autumn site.

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