Do humans adjust offspring sex according to the local operational sex ratio?

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ABSTRACT

Question: Do humans overproduce the rarer sex in response to skews in the local operational sex ratio (OSR)? And how should one define the OSR in humans?

Hypothesis: We predicted that instead of the current adult sex ratio used in previous studies as a cue for the local OSR, parents should use the offspring sex ratio of the immediate preceding cohorts (estimated by an average spousal age difference at marriage) that comprise the most potential mates for their offspring.

Organism: Two historical (1718–1890) Sami populations from Northern Finland.

Analytical methods: Multivariate linear dynamic regression models to examine the delayed ratio-dependence of annual offspring sex ratio at birth, while controlling for the potential effects of annual maternal and paternal age at reproduction and reconstructed mean ambient temperature.

Results: One of the two Sami populations studied showed evidence for the compensatory production of the rarer sex in relation to the skews in predicted local OSR.

Keywords: Fisherian sex allocation, maternal and paternal age, temperature, time-series analysis.

INTRODUCTION

If the operational sex ratio (OSR) of a population – the ratio of local males to females ready to mate at a given time (Emlen and Oring, 1977) – is biased from unity, parents are predicted to adjust their offspring sex ratio towards the rarer sex due to reduced fitness returns gained from the offspring of the overproduced sex (Fisher, 1930; Werren and Charnov, 1978; Charnov, 1982; Frank, 1990). The reduction in fitness among the more common sex is often linked to more intense mating competition and sexual selection (Emlen and Oring, 1977; Kvarnemo and Ahnesjö, 2002). The

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recent recognition that in many species offspring sex ratios may show even large temporal variation thus prompts deeper understanding on the nature and origin of sex ratio dynamics (Caswell and Weeks, 1986; Lindström and Kokko, 1998; Ranta *et al.*, 1999).

Despite rather intensive research efforts, there is currently limited evidence that parents adjust their offspring birth sex ratio according to the local OSR, often estimated as the concurrent sex ratio of adults. The few examples for vertebrates include a mouse lemur (Perret, 1990), some lizards (Olsson and Shine, 2001; Robert *et al.*, 2003; Warner and Shine, 2007), a lion (Creel and Creel, 1997), and a goshawk (Byholm *et al.*, 2002). Corresponding shifts in the offspring birth sex ratio have not been found in the other bird (Bensch *et al.*, 1999; Wheelwright and Seabury, 2003; Zann and Runciman, 2003) and lizard species studied (Le Galliard *et al.*, 2005; Allsop *et al.*, 2006), guppies (Brown, 1982; Pettersson *et al.*, 2004) or voles (Bond *et al.*, 2003). The proximate mechanism(s) by which parents might respond to variation in local OSR and adjust their offspring birth sex ratio accordingly remain unknown at present.

Lummaa *et al.* (1998) found that in pre-industrial Finland, skews in the human population adult sex ratio (individuals aged 15–50 years) were compensated by the production of offspring of the opposite sex in 14 of 21 populations studied. This inconsistency led Ranta *et al.* (1999), using the same data, to suggest that adjustment of the birth sex ratio may have occurred in response not only to local adult sex ratio, but also to the adult sex ratio of neighbouring populations. James (2000) was partly able to replicate the results of Lummaa *et al.* (1998) using nationwide data from 41 countries. However, as noted by James (2000) himself, nationwide data are inappropriate to infer birth sex ratio dynamics relevant to this hypothesis due to clearly separate mating pools across countries. There is also some indication of compensatory production of males during and immediately after wars that is compatible with the idea discussed above (e.g. Graffelman and Hoekstra, 2000; Polasek 2006).

The idea that parents use the local adult sex ratio as a cue for the OSR for their offspring is unlikely to hold in humans, as already noted by Lummaa *et al.* (1998). This is because when the currently born cohort reaches sexual maturity and marriageable age (which may range from 12 to 25 years, depending on the population), a large proportion of the adult population of their time at birth has already married, died, migrated or women have become post-reproductive. Therefore, the current adult sex ratio is likely to be a poor estimate of the true OSR of the offspring born. Instead, it is more reasonable to assume that the OSR consists of individuals born within the range of a population's average spousal age difference at marriage. That is, the most accurate cue for parents of the local OSR of their offspring is the birth sex ratio of those previously born cohorts that comprise the most potential mates for their offspring. Therefore, the OSR is likely to be population- and culture-specific, determined mainly by the local average spousal age difference at marriage.

To understand the temporal dynamics of human birth sex ratios in the light of the hypothesis introduced above, we investigated annual variation in offspring sex ratio at birth in two historical monogamous Sami populations from Northern Finland. We predicted that if parents adjust the sex of their offspring in relation to the sex ratio of preceding cohorts – that is, the local OSR predicted – we should find negative delayed ratio-dependence of annual birth sex ratios between consecutive years. The extent of the delay in years of this ratio-dependence should roughly match the population-specific average spousal age difference at marriage. If such an intrinsic process of birth sex ratio adjustment is repeated through time, oscillations of the birth sex ratio should appear (Turchin, 2003). However, to reveal the intrinsic dynamics of birth sex ratios, one should first control for any extrinsic factors potentially affecting the annual birth sex ratio (Turchin, 2003). Here, such extrinsic

factors may include variation in parental age at reproduction (Lazarus, 2002) and environmental variability such as ambient temperature, which has been shown to affect the offspring birth sex ratio among these Sami (Helle *et al.*, 2008).

METHODS

Study populations

Demographic data on two monogamous Sami populations from Northern Finland (Utsjoki and Inari for years 1745–1890 and 1718–1890, respectively) were extracted from historical parish registers kept by the Lutheran church (Helle *et al.*, 2002, 2008). These registers consist of continuous baptism, burial, and marital records from which we calculated the annual sex ratio at birth (the proportion of males born) and mean age for those parents who reproduced in a given year (Lazarus, 2002). Sami occupied large geographic areas where they practised mainly reindeer herding, fishing, and hunting for their livelihood and lived in small family groups or villages (Itkonen, 1948). Marriages between the two Sami populations were rare during the study period (Itkonen, 1948). The Sami people experienced natural fertility and mortality due to the lack of any advanced medical care or birth control methods (Itkonen, 1948). We are not aware of any sex-dependent infanticide that would confound our results. Descriptive statistics for these populations are given in Table 1.

Predicted delayed ratio-dependence of birth sex ratio series

To predict the population-specific patterns of the delayed ratio-dependence of annual offspring sex ratio at birth, we calculated average spousal age difference at marriage during the study period by subtracting wife's age from husband's age. In both populations, men married women slightly less than 3 years younger than themselves (Table 1). Using these mean spousal age differences and their standard errors, we predicted that in Utsjoki the birth sex ratio should show a negative correlation with the offspring sex ratio born *1–3* years

Table 1. Numbers of male, female, and total births (min, max), mean (± 1 s.d.) offspring sex ratio at birth and maternal and paternal age at reproduction, mean (± 1 s.e.) spousal age difference at marriage, and the coefficient of variation (CV) for selected variables

	Utsjoki	Inari
Male births	674 (0, 11)	1198 (0, 20)
Female births	615 (0, 11)	1189 (1, 20)
Total births	1289 (2,17)	2387 (2, 35)
Sex ratio at birth	0.52 (0.14)	0.50 (0.12)
Maternal age at reproduction	33.3 (2.5)	32.5 (2.0)
Paternal age at reproduction	38.1 (3.6)	37.1 (2.8)
Age difference at marriage	2.62 (0.72)	2.86 (0.39)
CV$_{\text{male births}}$	51.53	61.90
CV$_{\text{female births}}$	49.89	61.14
CV$_{\text{sex ratio at birth}}$	26.46	24.62

earlier. In Inari, corresponding associations should be seen between offspring birth sex ratio and the sex ratio born *2–3* years earlier.

The correlation between annual birth sex ratio and the sex ratio of offspring surviving to adulthood [age 18, which was commonly the earliest allowed marital age in these populations (Itkonen, 1948)] was strong (in both populations, Pearson's $r = 0.89$, $P < 0.0001$). Parents may have thus used the annual birth sex ratio of the preceding years as a reliable cue for the upcoming OSR of their offspring.

Environmental data

Because meteorological records in Northern Finland began in the early twentieth century, we had to rely on reconstructed climatic records, of which the most frequently used are tree-rings for annual summer temperatures (Briffa *et al.*, 1990; Esper *et al.*, 2002). Moreover, the NAO index, which describes the oscillation of atmospheric mass between the Arctic (Iceland) and the subtropical Atlantic (Azores), was used because it markedly dictates winter climate in North-West Europe (Hurrell *et al.*, 2001). The reconstructed NAO index of Luterbacher *et al.* (2002) since 1659 and two types of tree-ring chronologies of Scots pine (*Pinus sylvestris* L.) from Northern Fennoscandia were used: tree-ring width chronology of Helama *et al.* (2005) and maximum density chronology of Briffa *et al.* (1990). To reconstruct annual mean temperature (in Celsius) in the study region, these three data sets were integrated into one palaeoclimatic model using a linear regression (Helle and Helama, 2007). The reconstructed annual mean temperature is in good agreement with the observed annual temperature variability at nearby Karasjok weather station in Northern Norway between 1890 and 1978 [Pearson's $r = 0.72$, 95% confidence intervals $= 0.61$, 0.80, $P < 0.0001$ (Mudelsee, 2003)], indicating high reliability of the reconstruction. However, some uncertainty originating from potential non-climatic variability may be incorporated into the reconstruction. Regarding the NAO index, temporal instability of NAO climate associations may introduce some noise into the series (Luterbacher *et al.*, 2002). Regarding tree-rings, unwanted variability can arise due to the age of trees and inter-tree competition (Helama *et al.*, 2005). These factors were, however, taken into account in the standard tree-ring procedures used (Helama *et al.*, 2005).

Statistical analysis

We wanted to reveal the potential ratio-dependence of annual birth sex ratios by concentrating on modelling the residual autocorrelation of the series, after removing the potential effects of annual maternal and paternal age at reproduction and reconstructed mean temperature. The autocorrelation function gives the estimate of average correlation between the values of a series at time t and $t - i$, where i is any positive integer smaller than the length of the series, and is used to assess the periodicity of time-series. Strong evidence for a periodicity at a certain dominant cycle length is obtained if the autocorrelation function reaching its first maximum differs statistically from zero, while weak evidence for a periodicity is found if the autocorrelation function at its first minimum of estimated half-period only differs statistically from zero (Turchin, 2003). A related measure, the partial autocorrelation function, helps to determine the number of autoregressive terms (process order) needed to model the delayed ratio-dependence of the response series (Turchin, 2003), and is thus of most interest here. In addition to these autoregressive terms predicted by the local spousal age difference at marriage, we included, if necessary, additional autoregressive

terms into the models to account for the potential non-predicted autocorrelation of the residuals. Analyses were conducted with linear dynamic regression models with maximum likelihood estimation (Yaffee and McGee, 2000; Brocklebank and Dickey, 2003). Using this approach, one can relate variation in offspring birth sex ratio to the current and past values of explanatory variables. However, because it is difficult to see any biological relevance for the delayed effects of parental age at reproduction on annual birth sex ratio, we were interested only in synchronous variation in the birth sex ratio and parental reproductive age. On the other hand, since the current and previous year's temperature has been shown to correlate with annual offspring birth sex ratio among these Sami, we also included the previous year's mean temperature in our analyses (Helle *et al.*, 2008).

Prior to the analyses, stationarity of the birth sex ratio series was examined with (augmented) Dickey-Fuller tests (Yaffee and McGee, 2000; Brocklebank and Dickey, 2003). In Utsjoki, the test rejected a unit root stationarity of the response series (augmented Dickey-Fuller test, $P = 0.30$). Therefore, the series was differenced once to acquire a stationary mean (augmented Dickey-Fuller tests, $P < 0.0001$). That is, the birth sex ratio series was transformed by subtracting the past value from the current one ($Y_t = Y_t - Y_{t-1}$). Accordingly, in Utsjoki, the first difference was also taken from the explanatory variables (Yaffee and McGee, 2000). In Inari, Dickey-Fuller tests suggested that the birth sex ratio series was stationary ($P < 0.015$) and thus the analysis was performed on the original series. Furthermore, the response series were centred to their mean and thus the intercept was omitted from the models (Yaffee and McGee, 2000). Final models including statistically significant explanatory variables only were obtained by a backward elimination procedure. Before accepting these final models, the estimated parameters of explanatory variables were confirmed to be uncorrelated with the model residuals using cross-correlation functions (Yaffee and McGee 2000). This procedure tests for the potential unaccounted delayed effects of predictors on the response. The residuals of these models were normally distributed (Shapiro-Wilks test, $P > 0.13$) and homoscedastic (LaGrange multiplier tests for 12 orders, $P > 0.22$). Among independent variables, the largest inflation factor was 1.36 and the smallest tolerance value was 0.74, suggesting no bias in the standard errors of estimated regression coefficients. Analyses were conducted with the SAS statistical software package version 9.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Temporal fluctuations of annual offspring birth sex ratios are shown in Fig. 1. In Utsjoki, variation in the birth sex ratio tended to be slightly more related to variation of male than female births, whereas in Inari no such distinction between the sexes was apparent (Table 1).

After accounting for the potential effects of mean maternal and paternal reproductive age and ambient temperature, a delayed ratio-dependence of birth sex ratio was found in Utsjoki only. As predicted, in Utsjoki more males were born in relation to female-biased birth sex ratio during the previous 3 years and vice versa (Table 2). The magnitude of this delayed ratio-dependence decreased with the increasing lag. The fitted model explained almost 60% of the variation in annual birth sex ratio in Utsjoki. Furthermore, Fig. 2 suggests a periodicity of 2 years in Utsjoki. In Inari, annual offspring birth sex ratio was unrelated to its past fluctuations (Table 2).
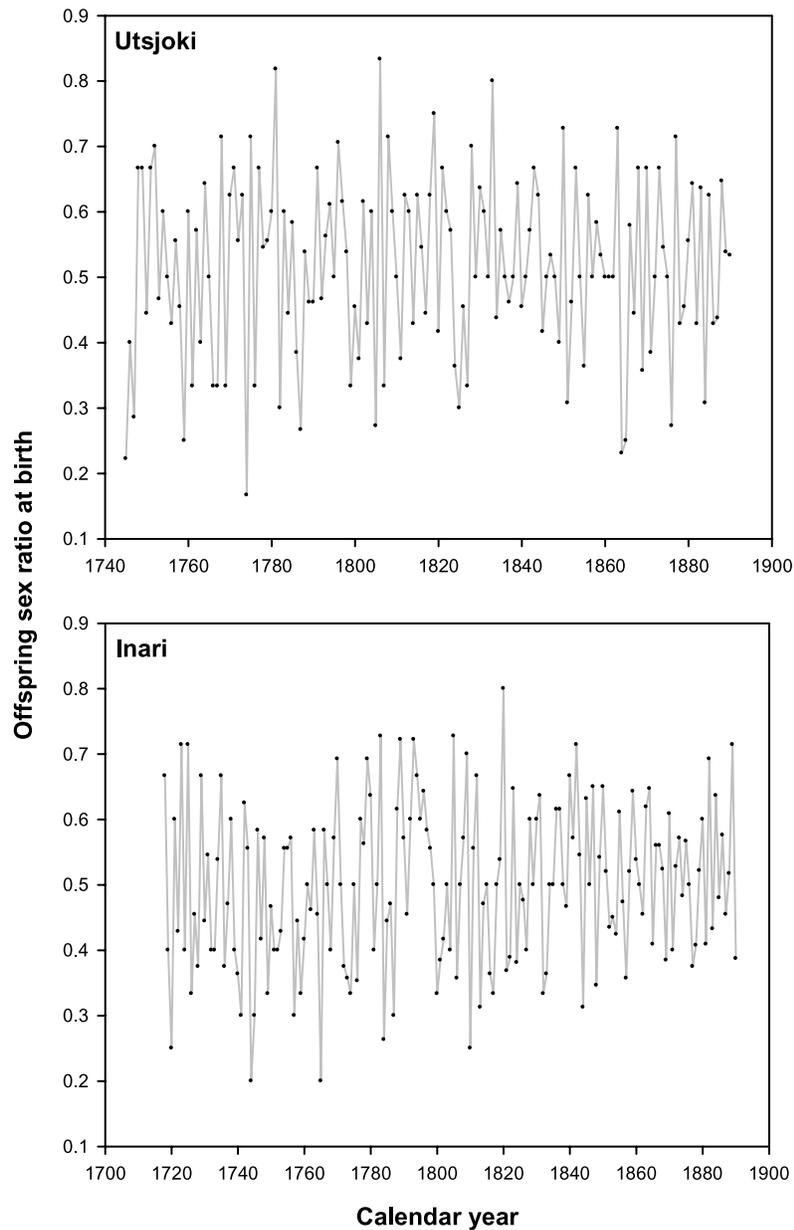
Fig. 1. Temporal variation in the offspring sex ratio at birth in the Sami populations studied (original data shown).

DISCUSSION

We found partial support for the Sami adjusting their offspring sex in relation to skews in predicted local OSR. In Utsjoki, but not in Inari, we detected a match between the predicted and observed delayed ratio-dependence of annual offspring birth sex ratio, as more

Table 2. The effects of the current and previous year's mean temperature, maternal and paternal age at reproduction, and the predicted autoregressive orders on annual sex ratio at birth

	Utsjoki			Inari		
	lag	β ($\pm$s.e.)	P	lag	β ($\pm$s.e.)	P
Mean temperature	**0**	**0.029 (0.012)**	**0.0197**	**0**	**0.024 (0.011)**	**0.0296**
	1	−0.024 (0.013)	0.0536	1	0.005 (0.011)	0.63
Maternal age	0	−0.003 (0.006)	0.59	0	0.005 (0.005)	0.32
Paternal age	**0**	**−0.010 (0.004)**	**0.0085**	0	−0.002 (0.004)	0.63
Autoregressive terms	**1**	**−1.004 (0.082)**	**< 0.0001**	2	−0.053 (0.078)	0.49
	2	**−0.605 (0.107)**	**< 0.0001**	3	0.010 (0.079)	0.90
	3	**−0.269 (0.082)**	**0.001**			
R^2		0.593			0.027	

Note: Explanatory variables included in the final minimal models are highlighted in bold. R^2 represents the coefficient of determination.

males were born in relation to female-biased birth sex ratio in the previous 3 years and vice versa. In Utsjoki, offspring sex ratio at birth also showed a periodicity of 2 years.

We predicted that if parents adjust their offspring sex according to biases in the local OSR to improve the mating opportunities of their offspring, we should find negative correlations between the current and past birth sex ratios with a delay roughly matching the average spousal age difference at marriage of the population studied. In Utsjoki, we found evidence for this prediction: an increased excess of male births followed female-biased birth sex ratios in the previous 3 years and vice versa. In Inari, no evidence for the predicted adjustment of the offspring birth sex ratio was observed. One potential explanation for why only the Utsjoki population showed delayed ratio-dependence of birth sex ratios might be that parents must have been able to accumulate information on the surrounding offspring sex ratio born to exhibit the sex ratio adjustment suggested here. The accuracy of such information may depend on how large a fraction of the juvenile population is known before the potential determination of offspring sex. Adjustment of offspring sex according to the local OSR may have thus been more likely in small than in large populations. Therefore, in Utsjoki, which was the smallest population and where the birth rate was almost half that of Inari, parents may have been able to know a larger fraction of offspring born in previous cohorts and thus have been more likely to respond to skews in juvenile sex ratios in a predicted manner.

When fluctuations of birth sex ratios are explained by the intrinsic regulation of negative delayed ratio-dependence, potential exogenous confounders should be accounted for. We did not find strong evidence to suggest that among the Sami parental age at reproduction influenced the offspring birth sex ratio (Lazarus, 2002). Only paternal age at reproduction was found to correlate with offspring birth sex ratio in Utsjoki. In contrast, mean temperatures seemed to affect birth sex ratios (for a more detailed discussion, see Helle *et al.*, 2008). If offspring sex ratio at birth is regulated by negative delayed ratio-dependence, oscillations of the birth sex ratio should appear (Turchin, 2003). These fluctuations should, however, eventually level off at unity (Fisher, 1930). The tendency of populations to evolve towards the equilibrium sex ratio has been previously demonstrated in flies (Carvalho *et al.*, 1998; Blows *et al.*, 1999) and fishes (Conover and
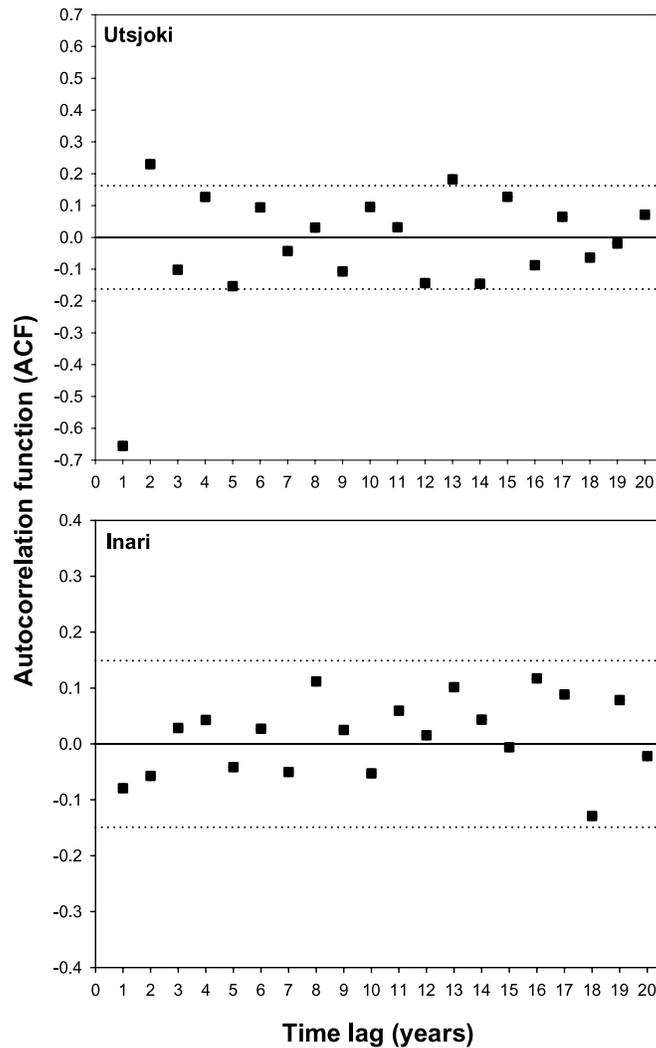
Fig. 2. Autocorrelation function plots of the annual sex ratio at birth after accounting for the potential effects of parental reproductive ages and mean ambient temperature (see Table 2), but not autoregressive factors. Dotted lines represent upper and lower 95% confidence intervals ($\pm 1.96 / \sqrt{2}$) of autocorrelation coefficients.

van Vororhees, 1990; Basolo, 1994). In Utsjoki, we found evidence for a periodicity of 2 years, but no indication that during the study period this variation in birth sex ratios would have levelled off (Fig. 1). This could suggest that in Sami offspring the sex ratio at birth was also affected by some unmeasured exogenous environmental and/or demographic factors that likely skewed birth sex ratios from unity in the first place and prevented them reaching and remaining at a stable level.

In conclusion, our results provide mixed evidence that Sami adjusted the sex of their offspring according to the birth sex ratio of previous cohorts (i.e. upcoming local OSR). We

emphasize that in applying this kind of ratio-dependent sex allocation model to the population-level patterns of birth sex ratio, it is crucial first to identify reliable and plausible cues available for parents to assess the relevant OSR for their unborn offspring. As argued here, such a cue is not the current adult sex ratio of the population, but the sex ratio of immediate preceding cohorts that included the most potential mates and competitors for the offspring born. Furthermore, because in these Sami, as in most human societies in general, men commonly marry younger women, it could be argued that parents should adjust the number of daughters rather than sons. This is because parents are mainly able to sample the proportion of potential husbands for their daughters (since they have already been born), not the future proportion of potential wives for their sons (since they have not yet been born). Among the Sami, there appeared however not to be a marked difference in variation of male and female births (Table 1). Due to this asymmetric mating pool between the sexes and the likely effects of temporarily variable migration and population size, it may become overwhelmingly difficult to demonstrate that humans have evolved to behave adaptively in this respect. We have currently very little evidence that humans adaptively adjust their offspring sex ratio in the first place (but see Bereczkei and Dunbar, 1997). In addition, we currently completely lack a potential mechanism(s) that could mediate the associations studied here.

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