

Sexually Coercive Male Chimpanzees Sire More Offspring

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Summary

In sexually reproducing animals, male and female reproductive strategies often conflict [1]. In some species, males use aggression to overcome female choice [2, 3], but debate persists over the extent to which this strategy is successful. Previous studies of male aggression toward females among wild chimpanzees have yielded contradictory results about the relationship between aggression and mating behavior [4–11]. Critically, however, copulation frequency in primates is not always predictive of reproductive success [12]. We analyzed a 17-year sample of behavioral and genetic data from the Kasekela chimpanzee (*Pan troglodytes schweinfurthii*) community in Gombe National Park, Tanzania, to test the hypothesis that male aggression toward females increases male reproductive success. We examined the effect of male aggression toward females during ovarian cycling, including periods when the females were sexually receptive (swollen) and periods when they were not. We found that, after controlling for confounding factors, male aggression during a female's swollen periods was positively correlated with copulation frequency. However, aggression toward swollen females was not predictive of paternity. Instead, aggression by high-ranking males toward females during their *nonswollen* periods was positively associated with likelihood of paternity. This indicates that long-term patterns of intimidation allow high-ranking males to increase their reproductive success, supporting the sexual coercion hypothesis. To our knowledge, this is the first study to present genetic evidence of sexual coercion as an adaptive strategy in a social mammal.

Results

The sexual coercion hypothesis predicts that male aggression against females increases male fitness [2, 10, 11]. We tested this prediction using behavioral and genetic data

from wild chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. Female chimpanzees exhibit an anogenital swelling for about 10 days within a 36-day ovarian cycle [13]. During this time, a female mates with most males in the community, although high-ranking males attempt to prevent this by directing aggression toward competitors and the female herself. We consider male-female aggression during the period of maximal swelling (“swollen aggression”) as potential short-term sexual coercion (but not as forced copulation, as males rarely attempt intromission during or immediately following aggression [11]). We consider aggression occurring outside this period (“nonswollen aggression”) as potential long-term coercion. Results support the hypothesis that aggression toward a given female functions as an intimidation strategy that increases a male's future chances of siring that female's offspring.

Aggression and Paternity

We used generalized linear mixed models (GLMMs) to analyze the relationship between aggression and likelihood of paternity within dyads. We included several additional potentially influential factors (see [Experimental Procedures](#)) and used Akaike's information criterion ($\Delta AICc$, a measure of the relative quality of a statistical model [14]) to identify the best predictors of paternity. Nonswollen aggression rate, male dominance rank, the interaction between these two factors, and dyadic relatedness were important predictors of paternity (Table 1; Figure 1A). Paternity probability was greater for males of higher rank (Figures 1A and 1C) but was lower if the male and female were closely related (Figures 1A and 1D). Males that were more aggressive toward females during nonswollen periods were more likely to conceive with those females. Although this relationship was positive for all males, it was particularly striking among high-ranking males—a high-ranking male with the greatest rate of nonswollen aggression had a 47.9% chance of conceiving with that female (Figure 1B). Among the subset of dyads in which the male's dominance rank score was one standard deviation above the mean (standardized rank score [MDS-Z] > 1, n = 47), there was a strong positive association between nonswollen aggression rate and paternity (Pearson correlation = 0.55, $p < 0.00001$; Figure 2).

Aggression and Copulation

We used GLMMs to identify predictors of copulation rate, and again used $\Delta AICc$ as the selection criterion. We identified both swollen and nonswollen aggression rates, female age, male rank, alpha male despotism ratio (see [Experimental Procedures](#)), relatedness, and two interaction terms as the best predictors of copulation rate (Table 2). Overall, males that showed higher levels of aggression toward females tended to copulate with those females at higher rates. However, swollen aggression had the strongest association with copulation rate. Copulation rates increased with female age but were lower in closely related dyads and during periods when the alpha male was particularly dominant (high despotism ratio).

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Table 1. Factors Influencing Likelihood of Paternity

Model	Fem Age	Rank	NS Agg	Parity	Despot Ratio	Relatedness	S Agg	NS × Agg Rank*	NS Agg × Relatedness*	AICc	Δ	Weight
1	–	1.26	1.06	–	–	0.17	–	1.48	–	204.83	0.00	0.287
2	–	1.19	1.05	–	–	–	–	1.55	–	205.81	0.98	0.176
3	–	1.26	1.06	0.88	–	0.17	–	1.49	–	206.76	1.93	0.109
4	–	1.25	1.05	–	–	0.16	1.05	1.48	–	206.77	1.94	0.109
5	1.00	1.26	1.06	–	–	0.17	–	1.48	–	206.79	1.96	0.108
6	–	1.26	1.06	–	0.99	0.17	–	1.48	–	206.82	1.99	0.106
7	–	1.26	1.05	–	–	0.17	–	1.48	0.90	206.82	1.99	0.106
Average	1.00	1.24	1.06	0.99	1.00	0.23	1.01	1.49	0.99	–	–	–

Models and effect sizes for averaged model and all models with $\Delta AICc \leq 2$. See [Experimental Procedures](#) for description of full model. Fem Age, centered female age (years); Rank, male standardized modified David's score (MDS-Z); NS Agg, standardized dyadic aggression rates toward females during their nonswollen periods; Parity, binary (1 = parous, 0 = nulliparous); Despot Ratio, despotism ratio, the ratio of alpha male MDS-Z to beta male MDS-Z; Relatedness, Queller and Goodnight's R; S Agg, standardized dyadic aggression rates toward females during their swollen periods. Columns marked with an asterisk (*) represent first-order interaction terms. Effect sizes are multiplicative effects on paternity odds ratio of a one-unit change in the variable. Values above 1 will increase likelihood of paternity, while values below 1 will decrease likelihood of paternity. In model 1, the only variable of the four significantly associated with likelihood of paternity was the interaction between male rank and nonswollen aggression ($p = 0.04$). In the averaged model, important predictors of paternity are indicated by *italics*.

Timing of Male-Female Aggression

To determine whether males directed more aggression at females when swollen than when nonswollen, we pooled data across the entire study period. Among dyads that spent ≥ 25 hr together during both swollen and nonswollen periods, swollen aggression rates were significantly higher than nonswollen aggression rates ($n = 549$ dyads, 2.3 [range 0 – 43.4] versus 1.5 [0 – 25.2] events per 1,000 hr together, Wilcoxon signed-rank test: $V = 32857$, $p < 0.001$). This pattern was driven by parous females; there was no difference between swollen and nonswollen aggression rates for nulliparous females ($n = 319$ dyads, 1.6 [range 0 – 22.2] versus 1.2 [0 – 25.2] events per 1,000 hr, Wilcoxon signed-rank test: $V = 6904$, $p = 0.13$).

Copulation and Paternity

Some primate studies have found little relationship between copulation rates and paternity [12, 15]. However, a model including the terms from the best model for predicting paternity (nonswollen aggression, relatedness, male rank, and male rank \times nonswollen aggression) demonstrated that copulation rate was significantly positively associated with paternity (GLMM, $z = 2.157$, $p = 0.03$).

Discussion

In this study of wild chimpanzees, aggression toward nonswollen females was positively associated with paternity, particularly among high-ranking males. This indicates that at Gombe, sexual coercion (as long-term intimidation) is a strategy that high-ranking males successfully employ to increase fitness. Male rank was also positively associated with paternity, independently of aggression. Although this could indicate female preference for dominant males, the relationship between aggression and paternity in high-ranking males indicates that patterns of paternity did not arise from unfettered female choice. Instead, the rank effect is most likely a consequence of mate guarding by dominant males [11, 16].

Copulation data also support the sexual coercion hypothesis. Males that directed high levels of aggression toward swollen females, and to a lesser extent nonswollen females, exhibited higher copulation rates. However, although copulation rate predicted paternity, males who were particularly aggressive toward swollen females were not more likely to sire those females' offspring. This is probably because swollen

females experience temporal variation in fertility, with fertilization most likely during the periovulatory period (POP) [17, 18]. Therefore, aggression toward swollen females may allow some (e.g., low-ranking) males to increase their mating success, but only during nonfertile portions of the females' swollen periods. This may also explain the finding that although males directed more aggression toward swollen females, only aggression toward nonswollen females increased paternity likelihood, especially for high-ranking males. Also, as the dominance of the alpha increased relative to other males, overall copulation rates decreased. This is intriguing evidence for effective mate guarding by strong alpha males and is consistent with previous work suggesting that alpha males sometimes trade mating access to females for coalitionary support [19]. "Despotic" alphas may need less support and thus may retain a greater share of copulations. As with paternity, male rank was positively correlated with copulation rate, probably due to mate guarding by high-ranking males.

This is the first genetic test of the sexual coercion hypothesis in any mammal. Importantly, our molecular and behavioral data accord extremely well with extensive behavioral evidence of long-term (indirect) sexual coercion in the Kanyawara chimpanzee (*P. t. schweinfurthii*) community in Kibale National Park, Uganda, where dyadic copulation rate and male aggression were also positively correlated [7]. As in our study, males displayed increased aggression toward parous females when they were sexually receptive. Additionally, copulations during the POP were correlated with aggression throughout the ovarian cycle [8], demonstrating the importance of long-term coercion at Kanyawara [11]. Higher-ranking males were the most frequent aggressors toward females [11], and when the alpha was present, there were fewer female solicitations (of other males) [8], demonstrating the alpha's effectiveness at mate guarding. Our finding that older females copulated more often than younger females is consistent with data from Kanyawara showing that older females are more attractive to males [20] and that parous females are more often the target of male aggression [21]. Such strong accordance between two research sites provides confidence in the robustness of these findings, certainly among eastern chimpanzees.

By contrast, research on western chimpanzees (*P. t. verus*) in Taï National Park, Côte d'Ivoire, found no evidence for sexual coercion, suggesting instead that females successfully employ mate choice [4–6]. There are several possible

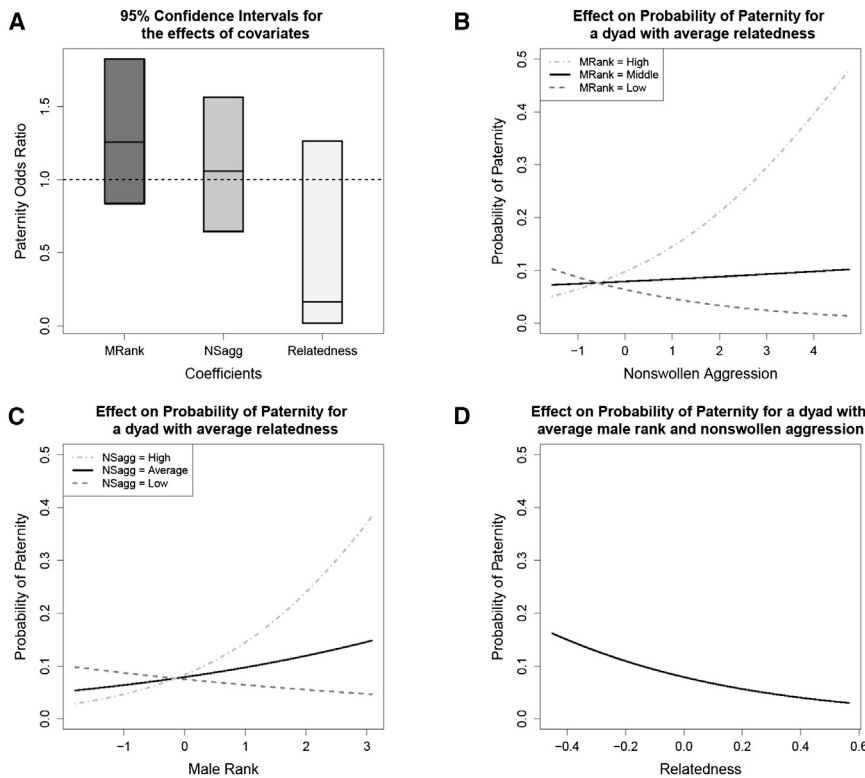


Figure 1. Predicted Likelihood of Paternity Based on Covariates from the Best Model

(A) Effect sizes and 95% confidence intervals of variables from the best model (model 1 in Table 1) on probability of paternity. MRank, male dominance rank (MDS-Z); NSagg, standardized nonswollen aggression rate; Relatedness, Queller and Goodnight's R (see Experimental Procedures).

(B) Lines represent the effect of aggression rates toward nonswollen females when all other covariates are at their average values. Solid line, middle-ranking males (MDS-Z = 0); dotted line, high-ranking males (MDS-Z = 1); dashed line, low-ranking males (MDS-Z = -1).

(C) Lines represent the effect of male rank (MDS-Z) on likelihood of paternity when other covariates are at their average values. Solid line, average levels of nonswollen aggression (NSagg = 0); dotted line, high levels of nonswollen aggression toward females (NSagg = 1); dashed line, low nonswollen aggression (NSagg = -1). (D) The effect of relatedness on likelihood of paternity among all dyads.

explanations for these contrasting results. At Taï, where females are more gregarious than at Gombe and Kanyawara [22], there may be fewer opportunities to “sneak” copulations in a more cohesive group, and thus less incentive for high-ranking males to use aggression to attempt to constrain female choice. Furthermore, our study community had similar numbers of adult males to Kanyawara (11–14 and 10–11 adult males, respectively) [7, 8] but more than double the number of adult males found in the two Taï communities studied (3–4 adult males) [6]. In smaller groups, reproductive success tends to correlate more closely with rank than in larger groups [12, 21, 23]. Thus, a high-ranking male in a small group may not need to resort to coercion to obtain a large share of paternities.

More comparative work is needed to disentangle the effects of biological and demographic differences on the prevalence and efficacy of male sexual coercion. Although the results from Gombe and Kanyawara clearly demonstrate that sexual coercion can be an effective component of sexual selection in chimpanzees, it remains to be seen whether coercion is a ubiquitous phenomenon, and whether alternative strategies exist. Further work is also needed to determine the mechanism by which long-term patterns of aggression increase paternity probability. Understanding the context in which nonswollen aggression by high-ranking males occurs and how those males interact with female recipients of coercion during swollen periods may shed light on why this strategy is effective for only some individuals.

Experimental Procedures

We used data from the long-term study of the Kasekela community at Gombe National Park. We analyzed data from a 17-year period (1995–2011) for which relatedness and paternity information was available from analysis of DNA obtained from fecal samples [24, 25]. During daily, all-day

focal follows of adult chimpanzees, researchers continuously recorded group composition, reproductive state of all females, and all observed aggressive and copulation events in the focal chimpanzee's party [13, 26]. We restricted analyses to “reproductive windows,” i.e., when a given female was experiencing ovarian cycles. For nulliparous females, this period started at sexual maturity and ended with their first conception. For parous females, this was the interval between the first sexual swelling after postpartum amenorrhea and the next conception. We estimated conception dates by backdating 226 days from the offspring's date of birth [27].

For analysis of copulation rates and paternity odds, we used data from reproductive windows during which offspring of known paternity were conceived, and from those dyads observed together during both swollen (mean ± SD = 275 ± 271 hr) and nonswollen periods (312 ± 283 hr). The difference between these two means is not statistically significant ($t = -1.7568, p = 0.079$). Adult males were at least 12 years of age, the age of the youngest known sire at Gombe [24, 25]. We classified females as adult after their first copulation with an adult male (for natal females) or immigration date. The data set contained 31 reproductive windows (among 21 adult females) and 18 adult males, forming 250 unique dyads and 338 dyad-reproductive windows.

We defined aggressive events as directed displays, chases, or contact aggression by one or more males toward a single female. We calculated rates of aggression for each dyad (aggression events per 1,000 hr together) and then standardized them by Z-transformation within each reproductive window. Thus, dyadic aggression rates represented a male's aggression rate relative to a female's average rate of received aggression from all males during a particular reproductive window. We classified aggression according to whether it occurred during the swollen period of a female's ovarian cycle (swollen aggression) or the nonswollen period (nonswollen aggression). Male rank was calculated for each window using the modified David's score (MDS) method [28], using submissive pant-grunt data from the year leading up to the end of the window. Because the maximum possible MDS in any period is proportional to the square of the number of individuals being ranked, we standardized the MDS scores by Z-transformation (MDS-Z) within each reproductive window to facilitate comparison between periods. We calculated a “despotism ratio” for each period to quantify the magnitude of rank difference between the alpha and beta male by dividing the MDS of the highest-ranking male by that of the second-highest. Finally, females were considered parous after having had one pregnancy carried to term and nulliparous otherwise.

To determine whether male aggression toward females increased in reproductive contexts, we pooled party association and aggression data for each dyad across the entire 17-year study period. Subjects for this

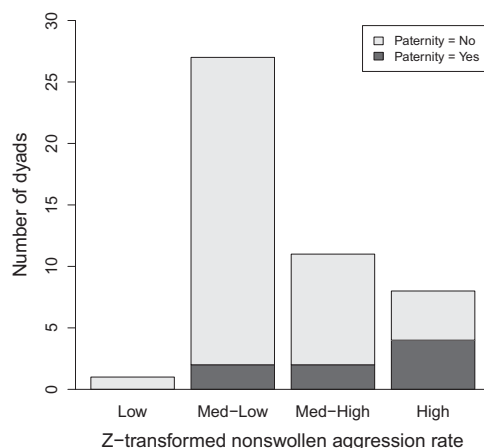


Figure 2. Paternity among Highly Ranked Males by Nonswollen Aggression Rate

Observed frequency of paternities among dyads with high-ranking males (MDS-Z > 1) versus nonswollen aggression rate. Low represents standardized aggression rates toward nonswollen females < -1; Med-Low: [-1, 0); Med-High: [0, 1); High: ≥ 1.

analysis were 38 cycling adult females and 20 adult males forming 549 dyads that spent at least 25 hr together during both swollen and nonswollen periods.

Of the 31 infants included in the study, paternities for 19 were previously reported by Wroblewski et al. [24] and for four by Gilby et al. [25]. Eight new paternities were identified for this study using DNA extracted from fecal samples. Fecal samples were collected and preserved in an equal volume of RNAlater (Ambion), and DNA was extracted using the QIAamp DNA Stool Mini Kit (QIAGEN) as described in Wroblewski et al. [24]. Individual genotypes were determined for 8–11 microsatellite loci through PCR amplification and allele sizing. Candidate males for paternity of each offspring were those that were ≥9 years of age at the time of conception. The offspring, mother, and candidate male genotypes were compared across all loci, and in every case, only one male (the father) could have contributed the complementary set of alleles to the offspring, given the maternal genotype. All other males had mismatches with the offspring and maternal genotypes at ≥1 locus. Relatedness between males and females was calculated using Kinship v1.3.1 [29] and is the

same as the frequency-based calculations established by Queller and Goodnight [30].

Analyses

For the GLMMs, we used swollen and nonswollen aggression rates to represent short- and long-term coercion efforts by males, respectively. We included in our full models the following factors, which, in addition to aggression, might influence paternity and copulation rates. Female age is known to influence male chimpanzee mating interest [20]. Male rank could increase dyadic paternity odds and copulation rates for dominant males via mate guarding [16, 31] or female preferences [32]. We included parity (nulliparous or parous) as a factor to determine whether it mediates the effect of male aggression on reproductive success as predicted by the “cost of sexual attractiveness” hypothesis [21]. As alpha males may trade mating access for coalitional support [19], a more despotic alpha may receive a higher share of paternities because he needs less support. Therefore, we calculated the despotism ratio (alpha MDS-Z/beta MDS-Z) for each reproductive window. Finally, we included dyadic relatedness because evidence from birds and mammals [32–35] suggests a cost to inbreeding, and Gombe chimpanzees are known to actively avoid mating with close relatives [35, 36]. We included all first-order interactions between both swollen and nonswollen aggression and these main effects, with the exception of despotism ratio. This we only included in a first-order interaction with male rank, as despotism ratio would seem unlikely to mediate the efficacy of male aggression.

All analyses were performed in R [37] using the lme4 package [38] for all GLMMs, and the MuMIn package for model selection [39]. For all models, we determined the best set of predictors using AIC as the model selection criterion [14, 40] and ranked the resulting models by ΔAICc, considering those with values ≤ 2 (with respect to the best model) to have substantial support [41]. We then used model averaging [41] to generate final parameter estimates based on this set of plausible models.

Paternity

To test whether aggression was correlated with likelihood of paternity, we ran a series of GLMM regressions, with paternity (yes/no) as the dependent variable, our candidate predictors of paternity and first-order interactions as factors, and female ID as a random effect. By standardizing aggression rates, we accounted for most of the variability that could be attributed to individual males. We therefore did not include male ID as a random effect in our final models, although inclusion resulted in minimal or no change in our parameter estimates.

Copulation Rate

To test whether aggression was correlated with copulation rates, we ran negative binomial GLMM regressions for count data (data overdispersion

Table 2. Factors Influencing Copulation Rates

Model	Fem Age	NS Rank	NS Agg	Despot Ratio	Relatedness	S Agg	NS Agg × Fem Age*	NS Agg × Rank*	Rank × Despot Ratio*	S Agg × Relatedness*	AICc	Δ	Weight
1	1.05	–	–	0.90	0.58	1.28	–	–	–	0.55	1610.53	0.00	0.15
2	1.05	1.23	–	0.90	0.55	1.28	–	–	0.95	0.54	1610.83	0.30	0.13
3	1.05	1.07	–	0.90	0.56	1.27	–	–	–	0.54	1610.85	0.32	0.13
4	1.05	–	1.06	0.90	0.59	1.27	–	–	–	0.56	1611.44	0.91	0.10
5	1.05	–	1.05	0.90	0.62	1.28	1.01	–	–	0.57	1611.56	1.03	0.09
6	1.05	1.07	1.06	0.90	0.57	1.26	–	–	–	0.55	1611.70	1.17	0.09
7	1.05	1.23	1.06	0.90	0.56	1.26	–	–	0.95	0.54	1611.71	1.18	0.08
8	1.05	1.23	1.05	0.90	0.58	1.27	1.01	–	0.95	0.55	1611.78	1.25	0.08
9	1.05	1.07	1.05	0.90	0.59	1.26	1.01	–	–	0.56	1611.92	1.39	0.08
10	1.05	1.22	1.06	0.90	0.59	1.26	–	1.06	0.95	0.51	1612.11	1.58	0.07
Average	1.05	1.10	1.03	0.90	0.58	1.27	1.00	1.00	0.98	0.55	–	–	–

Models and effect sizes for the average model and the best ten models. See [Experimental Procedures](#) for description of original full model. Fem Age, centered female age (years); Rank, male standardized modified David’s score (MDS-Z); NS Agg, standardized dyadic aggression rates toward females during their nonswollen periods; Despot ratio, despotism ratio, the ratio of alpha male MDS-Z to beta male MDS-Z; Relatedness, Queller and Goodnight’s R; S Agg, standardized dyadic aggression rates toward females during their swollen periods. Columns marked with an asterisk (*) represent first-order interaction terms. Effect sizes are multiplicative effects of a one-unit change in the variable on predicted copulation rates. Values above 1 will increase predicted dyadic copulation rates, while values below 1 will decrease predicted dyadic copulation rates. In model 1, swollen aggression rate is significantly positively correlated with copulation rate ($p < 0.000001$). Other factors significant in predicting copulation rate were female age ($p < 0.001$), despotism ratio ($p = 0.04$), and the interaction between swollen aggression rate and relatedness ($p = 0.03$). There was a trend toward significance for dyadic relatedness ($p = 0.07$). In the averaged model, important predictors of paternity are indicated by *italics*.

prevented the use of Poisson regression), with copulation counts as the outcome variable, time spent together as an offset, female ID as a random effect, and our candidate predictors of copulation rate (and first-order interaction terms) as factors. We did not account for zero inflation because the zero-inflated model produced no increase of fit over the standard model.

Copulation Rate versus Likelihood of Paternity

To test whether copulation rates were positively correlated with likelihood of paternity, we ran a logistic GLMM regression, with paternity (yes/no) as the outcome variable, female ID as a random effect, and the four terms from the best model for predicting paternity, plus copulation rate, as factors.

Accession Numbers

Data sets for aggression rate by swollen state and the regression analysis have been deposited in the Dryad Digital Repository with the DOI <http://doi.org/10.5061/dryad.v4h76>.

Author Contributions

J.T.F., A.E.P., and I.C.G. designed the project. E.E.W., R.S.R., and B.H.H. assigned paternities and calculated relatedness values. M.C.-R. and T.P. designed and implemented the regression analyses. All authors analyzed data. J.T.F., A.E.P., and I.C.G. wrote the manuscript with input from E.E.W. All authors read and commented on the manuscript.

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